

PROCEEDINGS OF
THE LINNEAN SOCIETY OF LONDON
 164th Session (1951-52)

Vol. 164

Part 2

CONTENTS

	Page
<i>PROCEEDINGS, 7 FEBRUARY 1952 to 24 MAY 1952</i> , including papers printed in abstract.....	99
Papers printed in full,—	
Edward Morgan and the Westminster Physic Garden. By R. H. JEFFERS, F.L.S.	102
A SYMPOSIUM ON PHOTOPERIODISM :	
Some recent experiments bearing on theories of Photoperiodism. By P. F. WAREING and D. J. CARR.....	134
Photoperiodism in the Chrysanthemum and its relation to Vernalization. By W. W. SCHWABE.....	135
Photoperiodism and Vernalization in Cereal Plants. By O. N. PURVIS	136
Photoperiodic responses of <i>Arabidopsis thaliana</i> . By F. G. GREGORY and G. G. HUSSEY.....	137
GROWTH AND SYSTEMATICS : JOINT DISCUSSION WITH THE SYSTEMATICS ASSOCIATION :	
Growth and body proportions in relation to the Systematics of the higher primates. By W. E. LE GROS CLARK.....	140
Relative growth in shells of the fossil family Anthracosiidae in upper carboniferous times. By R. M. C. EAGAR.....	148
Growth and Plant Systematics. By R. MELVILLE.....	173
Collecting Ferns in the mountains of the New World Tropics. By P. R. BELL	183
A survey of the Ecology of the British Lowland Bogs. By FRANCIS ROSE	186
SYMPOSIUM ON THE FORM AND FUNCTION IN THE MOLLUSCS :	
Form and Function in the Molluscs. By ALASTAIR GRAHAM.....	213
The transference of sperm from male to female prosobranch, with reference, also, to the Pyramidellids. By VERA FRETTER.....	217
On the feeding habits and the morphology and mode of functioning of the alimentary canal in some littoral dorid nudibranchiate mollusca. By J. E. FORREST.....	225
The chromatophore system of Cephalopods. By B. B. BOYCOTT.....	235
The functions of the Gastropod stomach. By J. E. MORTON.....	240
ANNIVERSARY MEETING	247
PRESIDENTIAL ADDRESS :	
Comparative studies in a Polyphyletic group. The Desmidiaceae.....	258
Obituaries.....	280
Additions and Donations to the Library.....	285
Benefactions.....	293

NOTE

Index, Title-page and Contents to Vols. 163 and 164 to be issued later.

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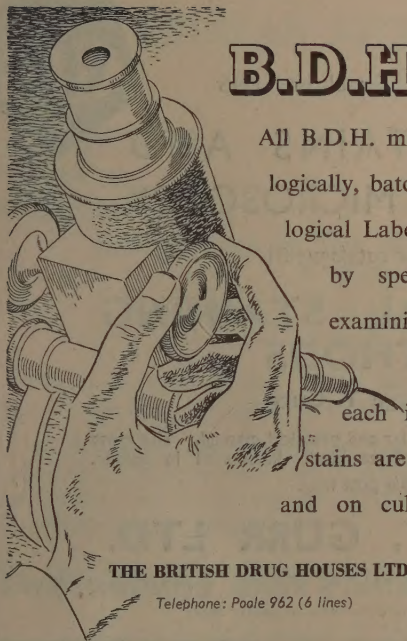
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PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

Session 1951-52

Vol. 164

Part 2

PROCEEDINGS OF THE GENERAL MEETING HELD 7 February 1952

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 24 January 1952, having been circulated, were taken as read, and confirmed.

The President announced the death of HIS LATE MAJESTY KING GEORGE VI, Patron of the Society, and read Addresses of Condolence with HER MAJESTY THE QUEEN, HER MAJESTY QUEEN ELIZABETH, and HER MAJESTY QUEEN MARY, all present rising in their places.

To the Queen's Most Excellent Majesty

THE HUMBLE ADDRESS OF THE PRESIDENT, COUNCIL, AND
FELLOWS OF THE LINNEAN SOCIETY OF LONDON

Most Gracious Sovereign

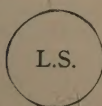
We, Your Majesty's most dutiful and loyal subjects, the President, Council, and Fellows of The Linnean Society of London in General Meeting assembled, humbly beg leave to offer our deepest and most heartfelt sympathy with Your Majesty in the great sorrow that has befallen You in the death of Your well beloved Father, our late Sovereign Lord, King George the Sixth. Your Majesty's loss is felt not only throughout the Commonwealth and Empire, but by the whole world.

While thus expressing our sorrow, we ask leave, Madam, at the same time to tender to Your Majesty our unfeigned and loyal homage upon Your Majesty's accession to the Throne of Your Ancestors.

The sympathetic interest, which Your Majesty has constantly manifested in all that concerns the progress of Science and its application to human life, encourages us to hope that Your Majesty will be graciously pleased to continue to our Corporate Body that beneficent Patronage which it has continuously enjoyed at the Hands of Your Majesty's Royal Predecessors since the granting of our Charter in 1802.

That Your Majesty's Reign over a loyal, grateful, and loving people may be long and glorious, is our dearest wish and ardent prayer.

Given under the Common Seal of the Society, this seventh day of February in the year one thousand nine hundred and fifty-two.



F. E. FRITSCH, *President.*

F. C. STERN, *Treasurer.*

A. TINDELL HOPWOOD, } *Secretaries.*
GEORGE TAYLOR, }

To Her Most Excellent Majesty Queen Elizabeth

THE HUMBLE ADDRESS OF THE PRESIDENT, COUNCIL, AND
FELLOWS OF THE LINNEAN SOCIETY OF LONDON

Madam

We the President, Council, and Fellows of The Linnean Society of London in General Meeting assembled, remembering with heartfelt pride the high distinction which Your Majesty conferred upon our Society in graciously consenting to become one of our Honorary Members, beg leave humbly to offer our profound and heartfelt sympathy with Your Majesty in the great and irreparable loss that has befallen You, the Royal House, and the Commonwealth and Empire, in the death of our Beloved and Venerated Sovereign Lord, King George the Sixth, our Patron, Whose Memory will ever be faithfully cherished by a grateful people.

Given under the Common Seal of the Society, this seventh day of February in the year one thousand nine hundred and fifty-two.

L.S.

F. E. FRITSCH, *President*.

F. C. STERN, *Treasurer*.

A. TINDELL HOPWOOD, } *Secretaries.*
GEORGE TAYLOR, }

To Her Most Excellent Majesty Queen Mary

THE HUMBLE ADDRESS OF THE PRESIDENT, COUNCIL, AND
FELLOWS OF THE LINNEAN SOCIETY OF LONDON

Madam

We the President, Council, and Fellows of The Linnean Society of London in General Meeting assembled, remembering with heartfelt pride the high distinction which Your Majesty conferred upon our Society in graciously consenting to become one of our Honorary Members, beg leave humbly to offer our profound and heartfelt sympathy with Your Majesty in the great and irreparable loss that has befallen You, the Royal House, and the Commonwealth and Empire, in the death of our Beloved and Venerated Sovereign Lord, King George the Sixth, our Patron, Whose Memory will ever be faithfully cherished by a grateful people.

Given under the Common Seal of the Society, this seventh day of February in the year one thousand nine hundred and fifty-two.

L.S.

F. E. FRITSCH, *President*.

F. C. STERN, *Treasurer*.

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GEORGE TAYLOR, }

The reading of the Addresses being concluded, the company remained standing in silence for a space.

The company having resumed their seats, the PRESIDENT adjourned the Meeting to a date to be announced.

**PROCEEDINGS OF THE GENERAL MEETING HELD
21 February 1952**

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 7 February 1952, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mrs. G. Montgomery, Dr. R. E. Schultes, Professor F. E. Weiss, F.R.S., Royal University, Uppsala, Fulham Public Library, British Association for the Advancement of Science, and Messrs. Thomas Nelson & Sons, Ltd.

The following signed the Obligation in the Roll and Charter Book, and was admitted a Fellow :—Miss Ruth Mary Badcock, M.Sc.

The PRESIDENT reported the death of Walter Robert Ivimey Cook, Fellow of the Society.

The following candidates for Ordinary Associateship were balloted for and elected. Kenneth L. Alvin, B.Sc., Raymond Harvey, B.Sc. and Miss Alice Barbara Patricia Stevens, B.Sc.

The following communication was read and discussed :—

Dr. S. M. MANTON, F.R.S. Developments and Science in the Soviet Union. (Discussed by Mr. Patrick M. Synge, Dr. J. Ramsbottom, O.B.E., Dr. W. H. Thorpe, Dr. E. M. Delf, Mr. G. S. Cansdale, Miss P. Whitby, Mr. R. J. G. Savage, Dr. George Taylor, Mr. F. C. Grigg and Mr. W. T. Stearn ; Dr. Manton replied.)

Abstract, —

Last summer I was invited to visit the Soviet Union. I met many scientists, visited the new university building in Moscow, research laboratories, and field stations, and travelled freely for 10,000 miles. I saw something of the pure and applied biological research and of the plant breeding.

Afforestation schemes were started in 1948 and hydro-electric projects in 1950 which, by 1957, will irrigate an area of 70 million acres, equal to one-third of the present irrigated lands of the whole world. The new irrigated areas and new pasture will make possible the production of food for 100 million people. The colossal construction schemes now under way involve sixteen times the earth work needed for the construction of the Panama canal, and will provide an annual output of 22,000 million k.watt hours.

The climate over large areas of the southern steppes and central Asian deserts is being changed. Rivers are being diverted ; dams are being built forming reservoirs up to 375 miles long ; thousands of miles of canals are being constructed, the larger carrying eleven times the flow of water transmitted by the Thames ; and forest belts 3,300 miles long are being planned.

An outline was given of the biological research which has been completed and is being carried out, in association with the transformation of the flora and fauna of steppe and desert. Reference was made to some aspects of the freshwater biological work connected with the expansion of fresh waters ; with the exploitation of the inland seas and introduction of marine invertebrate animals into these seas ; to the plant breeding and other work connected with the utilization of the altered territory ; to the work of 22 expeditions of

botanists and zoologists which have been working in the central Asian regions in the summer of 1951; and to the activities of the scientific research institutes in central Asia by Asian races. (A fuller account appears in *Nature, Lond.*, **167**, 729 (1952) and Manton, S. M., *The Soviet To-day*, London, 1952.)

The following papers were read in title :—

- 'Origin, distribution and phylogenetic affinity of the species of *Mangifera* Linn.' By S. K. MUKHERJEE, D.Sc. (Communicated by Dr. P. N. Bhaduri, F.L.S.) [Published in *Journ., Bot.*, No. **356**.]
- 'Edward Morgan and the Westminster Physic Garden.' By R. H. JEFFERS, F.L.S.
- 'Observations on the premaxillary dentition of snakes, with special reference to the egg-tooth.' By MALCOLM A. SMITH, F.L.S., A. D'A. BELLAIRS, F.L.S. and A. E. W. MILES. [Published in *Journ., Zool.*, No. **285**.]
- 'A new Pomadasid fish from the Colombian Caribbean.' By CECIL MILES, F.L.S. [Published in *Journ., Zool.*, No. **285**.]
- 'On the occurrence of pineal cartilages in the chondrocranium of a mammal.' By F. C. ELOFF. (Communicated by Prof. J. D. Boyd, F.L.S.) [Published in *Journ., Zool.*, No. **285**.]

EDWARD MORGAN AND THE WESTMINSTER PHYSIC GARDEN

By R. H. JEFFERS, F.L.S.

(With 1 text-figure.)

I. EDWARD MORGAN (c. 1619 to c. 1689).

Though nothing is known of his parentage, it is possible that Edward Morgan was born in North Wales, in, or more likely just before, the year 1619. Of his early years no particulars are available.

He is, in fact, first heard of in the year 1639, when, together with Paul Sone, he accompanied Thomas Johnson on a tour of North and Central Wales in search of plants. Johnson published an account of the journey, together with a list of the plants found (Johnson, 1641), from which it appears that Morgan, who is described as "rei herbariæ studiosus", accompanied the party as an interpreter in consequence of his knowledge of the Welsh language. The party left London in July 1639, and was joined at Chester by the Rev. Walter Stonehouse, a Londoner by birth, who had journeyed thither from his rectory at Darfield in Yorkshire, where he had a garden well stocked with plants (Gunther, 1920).

The details of the Welsh tour need not be considered here, but it should be noted that, at one point, the travellers were entertained by Robert Wynn, at Bodysgallen, near Aberconway, and that the Rev. Walter Stonehouse parted from them at Guerndhee, near Monmouth, and returned to Darfield. Johnson, Sone and Morgan travelled via Leominster, Hereford, Gloucester and Oxford, reaching London just after the middle of August. At Guerndhee Johnson found *Persicaria siliquosa* (Gerard, *Herball*, p. 446) [*Impatiens Noli-Tangere* L.], and included it in his list of plants (Johnson, 1641).

This journey differed from the previous expeditions in search of plants which Johnson had undertaken, in that neither of his companions seems to have been an apothecary. Morgan and Sone appear to have been young men, probably twenty years of age or so, and Morgan was quite likely living in Westminster, in the parish of St. Margaret's. It was in this parish that

Johnson had served his apprenticeship as an apothecary, from 1620 until 1628, under William Bell, but in 1639 Johnson was in business on Snow Hill, in the City of London (Kew & Powell, 1932).

Possibly as a result of his meeting with Stonehouse in 1639, Morgan sent to him, in 1640, a plant of *Dororicum Americanum* (*Rudbeckia laciniata* L.), which Stonehouse grew in his garden at Darfield (Gunther, 1920). It is not known whence Morgan secured the plant, though it was grown by John Parkinson, who, at this time, still had his house and garden in Long Acre—not very far from Westminster. No evidence is so far available that Parkinson and Morgan were acquainted.

A period of ten years now elapses before Edward Morgan is heard of again. Johnson, however, remained in London until December 1642, but seems to have gone to Oxford early in 1643, where he received a commission in the Royalist Army. He took part in the Siege of Basing House, and succumbed to wounds received during the final phase of the Siege. He died in September 1644 (Kew & Powell, 1932).

Among the postgraduate students at the University of Oxford in 1643 was William Howe, who early espoused the Royal cause and received a commission in the Army; but with the decline in the Royal fortunes he gave up his commission and returned to the study of medicine (Jackson, 1908). It is not known when this took place, but it may have been in 1645 after the decisive Battle of Naseby. At the close of the Civil War, Howe settled in London where he practised medicine. By 1648 he was in correspondence with Walter Stonehouse, from whom he received dried specimens of a species of *Trifolium*. It is, perhaps, not without significance that Stonehouse, an Oxford graduate and a friend of Johnson, was also a Royalist.

In 1650 William Howe published his *Phytologia Britannica*, to his own copy of which he added some manuscript notes which have been printed (Gunther, 1922). They contain a list of plants, some of which are recorded as found by Edward Morgan, while of others he requires from Morgan particulars of their habitats. This list of Morgan's plants is reproduced below, and shows that by this time he was a good field botanist. Howe also possessed what is believed to be Thomas Johnson's own copy of his *Descriptio in Agrum Cantianum* (1632), to which he had added a manuscript index, believed to be in his own hand. This index was extended by Howe, who added some manuscript notes. These have also been printed (Gunther, 1922) and one note reads :

“Consult Morgan about Orchis.”

As Gunther points out, both sets of notes were prepared between 1650 and 1656, though they cannot be more accurately dated. On the other hand, they reveal that soon after 1650, if not before, William Howe and Edward Morgan had become acquainted.

On 20 September 1655, Howe wrote to Dr. (later Sir) Thomas Browne at Norwich (Wilkin, 1852), acknowledging the receipt from him of “*Pimpinella moschata* sive *Agrimoniae folio quorundam Agrimoides*, Fab. Columnæ minus cognit. stirp. pag. 145” (*Pimpinella hybridum* L.), which he grew in his garden. It is in this letter that Howe gives an outline of his scheme for preparing a Catalogue of Plants, which were apparently growing in the “Westminster Garden for horticulture, medicine, and perfumery”, though it throws no light upon his connection with it. Browne himself, in a letter to Dr. Christopher Merrett, mentions sending to Howe plants of *Acorus Calamus* L. and it is interesting to note that this species was grown by Edward Morgan at Westminster.

The death of William Howe, at a comparatively early age, occurred in 1656 (Jackson, 1908) and thus brought to an end his association with Edward Morgan and the Westminster Physic Garden. That he was, in fact, associated

with the Garden is made plain in *The Art of Simpling* written by William Coles and published in 1656. Coles, formerly of the University of Oxford, was at this time resident at Putney. In his book, William Howe is described as 'one of the Masters' of the Westminster Physic Garden, and Edward Morgan as 'Gardiner'. Who the other 'Masters' were is still unknown, but this is the first reference to Morgan's connection with the Westminster Physic Garden. It is reasonable to infer that the Garden had been in existence for some time, and that Morgan had held his post prior to 1655. This view receives further support from a study of William Coles' *Adam in Eden* published in 1657. The address 'To The Reader' states:

"... And now ingenuous Reader, that I may shew my selfe as sincere an honourer and true lover of the advancement of this Science as I can, give me leave most heartily to, with that there were more Benefactors to the late noble Institutions of some Physick Gardens; amongst which Mr. Morgan, of Westminster, hath one in his Tuition, which by the noblenesse of Dr. How, is already very full fraught, and is like to be rendered more richly fruitful."

The "Approbation of divers Herbarists concerning the ensuing Work" is signed:

"In Approbation and Testimony whereof we have thought good to own this Work, with the Subscription of our Names:

Edward Morgan, Herbarist
to the Physick Garden of
Westminster.

Thomas Gillbank.
Richard Tuggey.

Cum multis aliis."

Coles, in the text (p. 48), mentions that he had visited the Garden, and makes thirteen references to the plants grown there, while on p. 382 he discusses eight kinds of Birthwort (*Aristolochia* spp.), of which:

"I finde none of these growing naturally in England, but that with the Long Foot, which is said to grow beyond Reading, yet divers others of the sorts are to be found either in the Physick Garden at Oxford, or in Dr. Howe's Garden at Westminster, or in Mr. Tradescant's Garden at Lambeth, being brought thither either mediately or immediately from their naturall places."

The Westminster Physic Garden was clearly well established by 1657, and must have been founded some years earlier. Nor did Howe's death bring it to an end, for Morgan continued to be Gardener, as appears from the oft-quoted entry in the "Diary" of John Evelyn (Bray, n.d.):

"10th June 1658: I went to see the Medical Garden at Westminster, well stored with plants, under Morgan, a very skilful botanist."

Evelyn was, at this time, not long returned from the Continent.

Edward Morgan is next heard of nearly three years later, when the Rev. John Ward visited him at the Garden on 4 March 1661. The visit, which was followed by many others, is thus recorded by Ward in his "Diary":

"On Tuesday March ye 4th [1661] I was at Ed. Morgan's where I saw these rare plants following: Agrimonia odorata, pimpinella spinosa, morus, Cynaara and tapsia, or scorching fennel, with many other pretty plants as sorts of Smilax aspera, one more roundish leaves, ye other longer.

Ned Morgan tels me next, Dr. Modesy, Dr. Dale, Mr. Merrit and Mr. Goodyer,—ye 3 last were about a new phutologia 3 or 4 years agoe. Dr. Modesie coming to towne, Ned Morgan thinks they left of(f)."

John Ward had left Oxford in 1660, and came to London to study medicine. His "Diary" mainly consists of medical notes, which have been discussed already (Power, 1920), but it contains others relating to botany, gardening and theology. Sir D'Arcy Power has described the "Diary", and given some biographical details of its author, besides drawing attention to the references in it to Edward Morgan (Power, 1917, 1919). Ward, after taking Orders, became Vicar of Stratford-on-Avon in 1662, but he continued to visit Morgan at his garden at Westminster, whenever his business brought him to London, up till about 1666.

As Sir D'Arcy Power has pointed out, it is clear that John Ward and Edward Morgan soon became close friends. The above passage, a typical one, is significant in this connection. Dr. Modesy or Modesie is the name by which Ward refers, throughout the "Diary", to Dr. Robert Morison, who had left Blois in France, and came to London in August 1660, there to take up an appointment in charge of the Royal gardens which included the Royal Physic Garden in St. James's Park, near St. James's Palace (Greene, 1860). Here Ward visited him, on several occasions, in 1661 and 1662. The Privy Garden in Whitehall, to which Ward also refers, was still in existence, having been repaired during the Commonwealth. Immediately after the Restoration, therefore, there were three gardens in Westminster—Edward Morgan's Westminster Physic Garden, the Royal Physic Garden in St. James's Park, and the Privy Garden in Whitehall. This fact is important, since there has been a tendency to confuse the three gardens.

The three men referred to by John Ward in the above extract from his "Diary" were, of course, Dr. John Dale (died 1662), his friend John Goodyer (1592–1664) and Christopher Merrett (1614–1693), who eventually produced what amounts to another edition of Howe's *Phytologia*.

During March 1661, Ward paid four further visits to Morgan at the Westminster Garden, which was followed by others at times which cannot always be accurately dated.

Early in 1662 John Ray, then at Trinity College, Cambridge, paid a visit to a friend in Surrey, and on his way back through London visited Edward Morgan at the Westminster Garden in February 1662 (Gunther, 1937). He arranged to supply Morgan with a copy of his *Cambridge Catalogue*, and, during his visit, made "an exact survey of Morgan's garden", though no details of it are extant. Finding himself unable personally to supply Morgan with the Catalogue, he wrote to a friend in London, begging him to perform the service, at the same time referring to Morgan in terms which suggest that, by now, he enjoyed a considerable reputation as a botanist.

Probably as a result of the visit in February, Morgan sent plants to Ray in 1662 for his garden at Trinity College.

John Ward visited Morgan twice during June 1662, and paid a third visit on 3 July 1662. On 1 September 1662, after a visit to Stratford-on-Avon, he called on Morison once more, at the Royal Physic Garden, and took up his appointment as Vicar at Stratford-on-Avon towards the end of the year. He seems to have visited Morgan again towards the end of May 1663, and also about the end of November 1663. Though he seems to have been in touch with him in 1664, his next visit appears to have been in July 1666.

In or about 1666 Morgan had another visitor to his garden. This was a young man and fellow resident of Westminster, Dr. Leonard Plukenet. He had been educated at Westminster School, and having taken a medical degree abroad, afterwards settled down in St. Margaret's Lane, Old Palace Yard, where he had a small botanic garden, and also practised medicine (Woodward, 1909). The results of his botanical studies are set out in a series of works, published largely at his own expense, which contain references to Edward Morgan, his plants and his garden, which Plukenet visited from time to time

in order to collect specimens for his herbarium (Plukenet, 1691, 1696; *Herb. Sloane*, Vol. 83).

A further consequence of the death of William Howe was that the task of preparing a further list of British Plants was undertaken by Christopher Merrett in circumstances which have already been discussed (Raven, 1947). For this purpose he employed the erstwhile Cromwellian soldier, Thomas Willisel, and had assistance from contemporary botanists and naturalists. The passage in John Ward's "Diary" quoted above shows that the work had been commenced about 1657 in conjunction with Dr. John Dale and John Goodyer, but that when Dr. Robert Morison arrived in London in 1660, the task was abandoned. However this may have been, the preparation of a new list of British plants certainly went forward, and was completed.

The first printing of Merrett's *Pinax Rerum Britannicum* took place in 1666 but most copies are dated 1667. In the "Epistola ad Lectorem" he acknowledged assistance from Thomas Willisel and Yalden Goodyer (grandson of John Goodyer) among others, but does not mention Edward Morgan. In the text however, he names five of Morgan's plants, and refers to Morgan himself and the Westminster Garden. The relevant entries are reproduced below. It seems likely, therefore, that Morgan did not lend so much assistance in the preparation of the *Pinax* as did Willisel, which would explain the absence of any reference to him in the "Epistola".

Two years after the publication of Merrett's *Pinax*, John Ray paid a second visit to the Westminster Garden (Raven, 1942), as a consequence of which he received from Morgan more plants for his garden, which was now presumably at Black Notley in Essex, since Ray had left Cambridge by this time. In the following year, 1670, John Ray published his *Catalogus Plantarum Angliæ*, containing many references to Thomas Willisel, and one or two to Edward Morgan (Ray, 1670), whence it may be inferred that Morgan grew in his garden at Westminster plants collected by Thomas Willisel, whom he may have met during the time that Merrett was preparing his *Pinax*, if not earlier.

The next reference to Edward Morgan occurs in 1672 (Morison, 1672). Robert Morison had given up his appointments in London during 1669 and at the end of that year had taken up an appointment as the first Professor of Botany at Oxford, though he seems to have retained a house in London in Leicester Fields. In 1672 he published his *Plantarum Umbelliferum*, in the text of which he refers to Morgan, his plants and the Westminster Physic Garden. These references afford evidence that Morison was personally acquainted with Morgan, which is confirmed by passages in Ward's "Diary" in 1662. During a visit to Morison in that year at the Royal Physic Garden, St. James's Park, Ward notes: "He [Morison] commends Ned Morgan for ye best collection of plants in England"—a remark which seems to have impressed him as it is repeated in two other places in the "Diary". A further reference to Morgan and the Westminster Physic Garden occurs in a letter written in 1672 by Leonard Plukenet to John Ray (Lankester, 1898) concerning a species of *Phalaris*.

In the summer of 1672 there occurred an event which was significant for the future of the Westminster Physic Garden. Mr. Gape was then elected Master of the Society of Apothecaries, who, about this time, had decided to establish a Physic Garden at Chelsea upon land leased by them from Edward Cheyne (Barrett, 1905). Mr. Gape offered to wall the Chelsea Garden at his own expense, but after legal objections had been raised, the work was carried out and paid for by means of subscriptions contributed by members of the Court of Assistants. This course may have been all the more necessary through the death of Mr. Gape himself, since nothing seems to be known of him after 1673.

In 1676 the Society of Apothecaries acquired the remainder of a lease of a garden at Westminster belonging to Mrs. Gape, presumably the widow of the Master in 1672. This lease expired in 1678, and the Society had the option of removing the plants to Chelsea. In 1677 the Court Book of the Society contains a reference to a Mr. Morgan who claims consideration for his plants (Barrett, 1905), whence it has been assumed that he was Edward Morgan of the Westminster Physic Garden, and that he may have exercised some supervision over the Chelsea Garden in its early stages. This latter suggestion seems unlikely. The Quaker botanist, the Rev. Thomas Lawson, visited Edward Morgan at Westminster in 1677, and listed in his "Notebook" some of the plants which he found growing there (Raven, 1948). He names nearly five hundred plants, so that the Westminster Garden was still well stocked, while, at Chelsea, one Piggott was appointed the first gardener in or about 1677. Proving unsatisfactory, he was replaced by James Watts in 1678, the year in which Mrs. Gape's lease of her Westminster garden expired. The "Books of Accompt" for the Overseers of the Poor of the Parish of St. Margaret, Westminster, are extant, and show that in 1676 Mrs. Gape does not appear among those leasing property in Westminster. On the whole it would appear that the Society of Apothecaries did not acquire the lease of the Westminster Physic Garden, and that Edward Morgan was still there in 1678.

In the Sloane Herbarium in the British Museum (Natural History) are three volumes of plants labelled "Plants of the Westminster Garden". They are Volumes 24, 25 and 26 and a note in Volume 24 states that the Westminster Garden "continued as Physick Garden containing many rare plants till the year 1686 or 1687, when about the latter end the gardener began selling his rare plants, and a sort of Ale made of the roots of *Meum Athamasticum*". "During the time of its subsisting a Physick Garden there were cultivated in it the plants brought from Tanger [Tangiers] when in our possession [=1661-1684], Canada, [and] our Northern Plantations, which plants may be seen in these three Volumes bought of Mr. Rusholm, the last Gardener." This entry is initialled "M(atthew) M(aty) 17¹/₈ 57." Volumes 25 and 26 contain "Plants gathered at the Physick Garden in Westminster about the year 1687", similarly initialled and dated, but Volume 24 states, apparently in respect of the three volumes: "Plants gathered by Mr. Morgan or Mr. Rusholm at the Physick Garden at Westminster, named and pasted in three volumes." Additional material is preserved in Vol. 70. It is now clear that the Westminster Physic Garden remained in existence until towards the close of the year 1687, and that Edward Morgan was succeeded as Gardener by Rusholm. The garden was then closed and the plants sold or dispersed. A study of the list of plants in the Westminster Garden recorded, bed by bed, by Thomas Lawson in 1677 shows that the garden seems to have been in two parts, so that it is possible that one portion could have been leased by Mrs. Gape. If so, this might explain the entry in the Society's books in respect both of Mrs. Gape and Morgan.

Though it is unknown when Mr. Rusholm took charge of the Westminster Garden, it is probable that he did so shortly after 1678, for Edward Morgan apparently left Westminster and is next heard of in 1680 when he was working at Bodysgallen, Aberconway, in the garden of Robert Wynn whom he had met in 1639 when in the company of Thomas Johnson (Gunther, 1922). Here he received correspondence. Thomas Thornes wrote from Lleweni, on behalf of Sir John Salusbury, on 20 September 1680, addressing the letter to Edward Morgan "living at Bodesclen", and sending him plants. "Mr. Harrison, Will Tomas and Coocke" presented their services to him (Gunther, 1922). Friderick von Henrich Dorff wrote to Morgan at "Bod Skallen" (Druce & Vines, 1897, 1919). Edward Lhwyd, then at the Ashmolean Museum at Oxford,

also kept in touch with him, but in 1685 wrote to his kinsman David Lloyd concerning Edward Morgan from whom he had not heard for some time. In this letter he highly commends Morgan for his services to botany (Gunther, 1945).

Nothing further is heard of Edward Morgan until 1689 when part, at least, of his *Hortus Siccus* was presented to the Ashmolean Museum at Oxford (Druce & Vines, 1897, 1919; Gunther, 1945), whence it is a reasonable inference that his death occurred probably between 1685 and 1689, especially as Lhwyd expressed concern in his letter as to whether Morgan was still alive. Assuming he had a normal span of life his birth could not have been later than 1619, so that he would have been at least twenty years of age when he visited Wales in 1639 with Thomas Johnson.

Morgan's *Hortus Siccus* of about 2,000 specimens, now at Oxford, seems to be only a part of the whole. This collection has been described, and a few of its contents identified (Druce & Vines, 1897, 1919); two or three of the plants are known to have been grown by Edward Morgan at Westminster. Though this is very slender evidence, it seems that, taken in conjunction with the other facts set out above, Edward Morgan of Westminster, and he of Bodysgallen were, in fact, one and the same person. Further support for this view is afforded by a consideration of the *Hortus Siccus* at Oxford and the material in the Sloane Herbarium. The former was prepared by Edward Morgan between 1672 and 1682, and must therefore have been commenced when he was still at Westminster. It is curious that it should have been started in the year when the Society of Apothecaries elected Mr. Gape as Master and the formation of the Chelsea Garden was under consideration, though it may well have been merely a coincidence. The material in the Sloane Herbarium proves to have been started in 1666 and completed (by Rusholm) in 1687, thus covering periods earlier than, and also later than, that at Oxford. Hence the Sloane Herbarium material may have been put together, first by Morgan, and then completed by Rusholm. The Sloane Herbarium also contains a volume labelled "Rusholm's Westminster Plants", containing material which suggests that he was of less ability than Morgan. Volumes 24, 25 and 26 in the Sloane Herbarium contain many plants which are also recorded by Thomas Lawson as grown by Morgan in 1677, whence it seems probable that this material may be, in part, the work of Edward Morgan between 1666 and 1678.

Two of Morgan's contemporaries referred to him and his plants in works published after 1698, by which time his death has been presumed to have occurred. These authors were Leonard Plukenet and Jacob Bobart the Younger, both of whom were known to Morgan personally. The references by the former occur in two works (Plukenet, 1691; Plukenet, 1696) and by the latter in Morison's unfinished work, which he completed (Morison, 1699). Edward Morgan was also acquainted with Jacob Bobart the Elder and supplied plants to him for the Oxford Physic Garden (Miller, 1807).

Only two contemporary authors throw any light on the site of the Westminster Physic Garden, but the information is meagre. Morison in his *Plantarum Umbelliferum*, 1672, pp. 1-2, says: "in horto Edvardi Morgan pone cœnobium Occidentale Westminster dictum", while Plukenet contents himself with remarking that the garden was "pone Abbatiam" (Plukenet, 1696), whence it would appear that the garden was in the vicinity of the West Cloister of Westminster Abbey. In the Sloane Herbarium is a label in the handwriting of James Petiver which states: "This grew many years ago in old Mr. Edw. Morgan's most famous garden behind the Abbey wall at Westminster"—a statement which places it within the Precinct of the Abbey. In John Ward's "Diary" is an entry which appears to have been made about

1663, though it may have been written earlier, which reads: "Where is ye Sanctuary at Westminster?"—which suggests that it had been mentioned to him as a guide to the site of Morgan's garden. The Sanctuary was a ragstone building built for the purpose of affording sanctuary, which stood in Broad Sanctuary at its junction with what is now Princes Street, but in Morgan's time called Long Ditch. The site of this building was later occupied by the Westminster Hospital recently demolished. The Sanctuary building was opposite Dean's Yard, and seems to offer further support for locating the garden in this neighbourhood, probably on the site of what is now Little Dean's Yard.

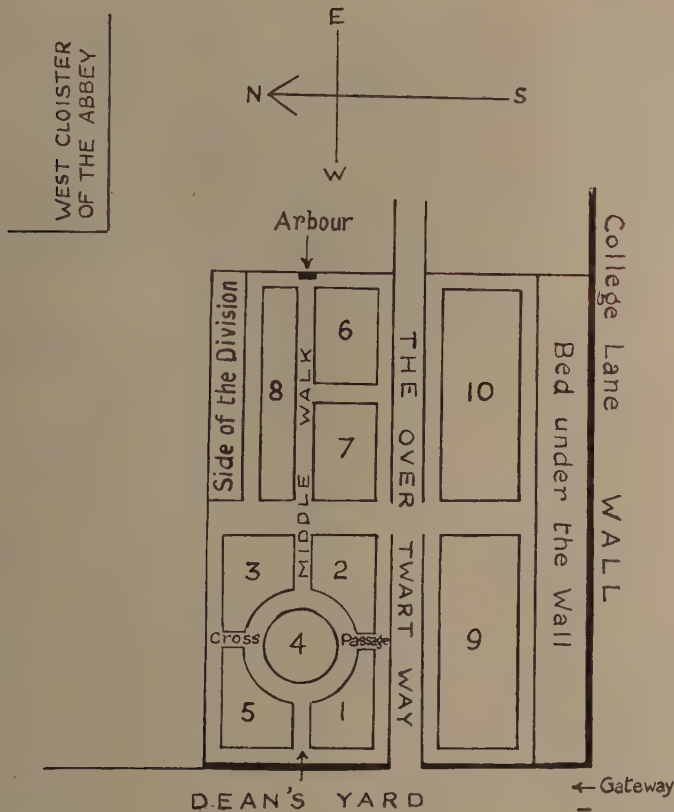


FIG. 1.—Reconstruction of a Plan of the Westminster Physic Garden from the Notes of Thomas Lawson and James Petiver.

It is possible, however, to form some idea of the character of the garden from the entries in Thomas Lawson's "Notebook". Though his notes are rather fragmentary, it seems likely that the Westminster Garden was modelled on that of Oxford, differing from it in that it appears to have been in two parts separated, the one section from the other, by what Lawson terms "the over thwart way". The garden may well have been rectangular, with rectangular beds intersected by paths, and from Lawson's reference to a wall, it seems possible that the old wall enclosing the Precinct of the Abbey may be intended.

A theoretical reconstruction of the plan of the garden has been attempted (fig. 1).

It is fitting to conclude this account of Edward Morgan and the Westminster Physic Garden with a reference to Morgan himself. He was held in high esteem as a botanist by his contemporaries, particularly by Thomas Johnson, John Ward, John Ray, Robert Morison, Jacob Bobart the Younger and Leonard Plukenet, as is evidenced by the references to him in their books. It is Edward Lhwyd, writing in 1685, to a kinsman (Gunther, 1945), who provides the best account of him:—

“ He is one that has lived in great esteem and one that in his way has deserved as well as any in England ; a man equally commendable for his good life and indefatigable industry. He has a studie of books worth abt. 10 li wch, he has told me several times he would leave me : if you can bring it in handsomely you may, with a safe conscience assure him that he cannot bestow em on one that wishes him better, nor perhaps on any friend yt will make better use of ym.”

Perhaps as a result of this letter Morgan's *Hortus Siccus* reached Oxford in 1689, but the fate of his library remains unknown.

No Catalogue of the plants grown in the Westminster Physic Garden appears to be extant, but an attempt has been made to provide first, a list of British plants found by Edward Morgan, and second, a list of the plants he grew in the Garden. These lists have been compiled from the following material:—

I. British Plants found by Morgan:—

- (a) Those recorded by William Howe in his manuscript notes (Gunther, 1922).
- (b) Those recorded by Christopher Merrett (Merrett, 1667).

II. Plants grown in the Westminster Physic Garden:—

- (a) Those recorded in the printed works of Morgan's contemporaries (Coles, 1657 ; Merrett, 1667 ; Ray, 1670, 1686 ; Plukenet, 1672, 1691, 1696 ; Morison, 1672, 1699).
- (b) Those recorded in Thomas Lawson's " Notebook ", 1677.
- (c) Those preserved in the Sloane Herbarium in the British Museum (Natural History). Only those definitely attributed to Morgan have been included.

The list of cultivated plants so compiled has been compared with contemporary books and catalogues, and reveals that the majority of the names in Lawson's list of 1677 may be found in Parkinson's *Theatrum Botanicum*, 1640, Morison's *Hortus Blessensis*, 1669, Tradescant's *Catalogue*, 1656, the Catalogue of the Oxford Physic Garden, 1658, and Caspar Bauhin's *Pinax* (second edition), 1656. It has also been compared with the *Book Herbarium* (c. 1660–1700) put up by the Bobarts, father and son (Savage, 1948). These comparisons suggest that Morgan may have received the greater part of his collection from Morison, when he was at Blois, and from the Bobarts at the Oxford Physic Garden, together with, in the early stages of the Garden, a few plants from the gardens of Parkinson in Long Acre and the Tradescants at South Lambeth.

Thomas Lawson records about five hundred plants growing at Westminster in 1677, which may have been perhaps a third of the total. At the outset the Garden may well have been a herb-garden, judging from the plants reported growing there in 1657 (Coles, 1657), though Howe's title for it suggests that its scope was intended to be much wider. By 1677, however, it seems to have developed into a botanic garden, in which were cultivated medicinal herbs, British wild plants, and plants from abroad, especially from Europe, Asia

Minor, Tangier and North America. Lawson's list includes only one species from South Africa, plants from which country began to reach Europe early in the seventeenth century, mainly through Holland, from the Dutch East India Company's settlement at the Cape. The total number of genera cultivated by, or collected by, Morgan amounts to just over two hundred and seventy.

II. PLANTS COLLECTED BY EDWARD MORGAN.

A. *British Plants found by Edward Morgan as recorded in William Howe's Manuscript Notes.*

1650-1656 (Gunther, 1922).

- Primula veris* flore pleno viridi } ? Morg[an] an. inser.
 ,, ,, sive *Paralysis fatua* }
 = *Primula veris* L.
Malva sylv. flore albo. Morg[an] = *Malva sylvestris* L., white flowered var. ?
Primula veris polyanthos M[organ] at Great Walford Wood (see the similar entry in Merrett's *Pinax*, 1677).
 = *Primula veris* L. var.
Carduus lanceolatus fl. alb. M[organ] St. James (see entry below).
Scabiosa ovilla flore albo M[organ] = *Jasione montana* L., white flowered var.
Primula veris Raii M[organ] Qu. loc. = *Primula veris* L. ?
Lychnis syl. : foliis variegatis fl. albo M[organ] Qu.
 = *Silene Cucubalus* Wibel (L.K.).
Cotula non fatida flore pleno latiore = *Anthemis nobilis* L.
Chamæbuxus fl. colutea Bauh : sive *Rhus* Plin : myrtifol :
 = *Polygala Chamæbuxus* L.
Carduus lanceolatus fl. alb. et fl. purp. Q. Chyrurg : for ye places of theese plants growth from Morgan. = *Cirsium lanceolatum* Scop.

B. *British Plants found by Edward Morgan as recorded by Christopher Merrett, 1667 (Merrett, 1667).*

- Malva arborea marina nostra* : Edward Morgan received it from the Isle of Wight
 = *Lavatera arborea*, L.
 (Morgan cultivated this plant which was still growing in the Westminster Garden in 1677, see Thomas Lawson's List.)
Persicaria siliquosa G[erard] 446. *Mercurialis sylv. noli-me-tangere dicta* P[arkinson] 296. "Within a mile of Montgomerie at Gwern Dhee [Werndhu] Mr. Morgan" (but found there by Thomas Johnson in 1639 and recorded by him in 1641, though Edward Morgan and Paul Sone were his companions at the time (Johnson, 1641)).
 = *Impatiens Noli-Tangere*, L.
Plantago ag. major muricata. "In a small pond betwixt Clapham and South Lambeth Common."
 = *Alisma Plantago*, L.
 (This entry suggests that Morgan while in this district may have visited the garden of the Tradescants at South Lambeth.)
Primula veris Polyanthos multis insignitur floribus quoad colorem et formam exacte resert *Primulam vulgarem*, sed compacti florescens ad instar *primulæ pratensis luteæ modoræ*. In great Woolver Wood in Warwickshire.
 = *Primula veris* L. var.
 (Morgan must have found this plant between 1650 and 1656 (vide Howe's MSS. notes above) if not earlier, and Merrett's record may be based on Howe's notes. Morgan grew the plant in the Westminster Garden, as Merrett here records, whence he has been regarded as the first cultivator of the Polyanthus, specimens of which from the Westminster Garden are to be found in the Sloane Herbarium.)

Fungus rotundus superna et translucidus coloris succinis. Mr. Morgan's garden.
= ?

Fungus campani formis niger parvus multa semina plana in se continens.
Mr. Morgan's garden, call'd in Wostershire. Corn-bells, where it grows
plentifully. = *Nidularia campanulata* Sow.

(These two entries relating to fungi are reproduced by Thomas Lawson
in his "Notebook", 1677, p. 97.)

III. PLANTS GROWN BY EDWARD MORGAN AT THE WESTMINSTER PHYSIC GARDEN.

A. Recorded by John Ward : March 1661 to July 1662.

Visit : 4th March 1661.

Agrimonia odorata

= *Agrimonia Eupatoria*, L. ?

pimpinella spinosa

= *Pimpinella spinosum*, L.

morus

= *Morus nigra*, L.

Cinara spinosa et aculeata

= *Acanthus spinosus*, L. and *A. spinosissimus*, L.

tapsia, or scorching fennel

= *Thapsia foetida*, L.

Smilax aspera

= *Smilax aspera*, L.

Visit : 22nd March, 1661.

Radix cava

= *Fumaria bulbosa*, L.

Bunias

= *Bunias Erucago*, L.

Visit : 24th March 1661.

Orobus

= *Orobus* sp.

Jeenetus panonicus

= ?

trifolium hemorrhoidale

= ?

Geranium fusca

= ?

Visit : 26th March 1661.

Cotyledon Mathioli

= *Saxifraga Cotyledon*, L.

Visit : [Spring], 1661.

Cinara spinosa et aculeata

= *Acanthus spinosus*, L. and *A. spinosissimus*, L.

Ilex coccigera

= *Quercus Coccifera*, L.

Ilex glandifera

= *Quercus Ilex* L.

Ilex aktae foliis

= ?

Visit : May, 1662.

Ornithopodium

= *Ornithopus perpusillus*, L.

gramen exile hirsutum

= ?

zancinus omnium minus

= ?

Lolium pumila

= ?

Medlar

= *Mespilus germanica*, L.

physick nut

= *Strycnos Nux Vomica*, L.

Spanish Jassemine

= *Spartium juncum*, L.

male pionis

= *Pæonia officinalis*, L.

female pionis

= *P. mascula*, Miller.

Lybian Poplar

= *Populus tremula*, L.

Lilium bulbosum

= *Lilium bulbiferum*, L.

Marsagon	= <i>Lilium Martagon</i> , L.
Gladiolus narbonensis	= <i>Gladiolus communis</i> , L.
Millefolium Aquaticum Ranunculi fol	
... capituli	= <i>Hottonia palustris</i> , L.
Gramen Avenaceum Parkinson	= <i>Avena elatior</i> , L. or <i>A. sterilis</i> , L.

Visit: June 1662.

Bird's eye	= ?
Glaux marina	= <i>Glaux maritima</i> , L.
napthor	= ?

Visit: 17th June 1662.

Bead tree	= <i>Zizyphus sativa</i> , Gaertn.
Glaux maritima	= <i>Glaux maritima</i> , L.
cruciata marina	= <i>Arenaria peploides</i> , L.

Visit: 3rd July, 1662.

absynthium arborescens	= <i>Artemisia arborescens</i> , L.
absynthium insipidum et inodorum	= <i>Artemisia Absynthium</i> L., var. <i>insipidum</i> DC.
Spanish Broome	= <i>Spartium junceum</i> , L.
Iberis Cordamantice	= <i>Lepidium</i> sp.
Acacia ffarnesiana	= <i>Acacia Farnesiana</i> , L.

Visit: [about July] 1662.

Glycirraza Cachinata	= <i>Glycyrrhiza echinata</i> , L.
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Visit: [date unknown].

Nasturtium Indicum	= <i>Tropæolum majus</i> , L. and <i>T. minus</i> , L.
Convolvulus cæruleus major	= ?

B. As Recorded by Thomas Lawson, 1677.

The list of plants seen at the Westminster Garden by Thomas Lawson in 1677 falls into two parts viz. :—

1. Three entries taken from Merrett's *Pinax*, and one from Ray's *Catalogue*, together with an odd note referring to Morgan himself which occurs in a list of plants found in Kent. Then follow a few plants noted at Westminster which occur in a list of Middlesex plants.
2. Then occurs a long list of plants seen at Westminster, together with a few duplicate entries.

The scattered notes are reproduced first, and followed by the main list, the pagination being that of the Notebook. About seventy of the plants in Lawson's list are British, the majority being plants of Europe, Tangiers and North America.

Thomas Lawson's "Notebook".

p. 97.

ffungus Campaniformis si[ve]. In	
Westminster Garden, Mer[rett].	= <i>Nidularia campanulata</i> , Sow.
ffungus rotundus superus concavus	
si[ve]. Westminster Garden,	
Mer[rett].	= ?

p. 100.

Malva arborea marina nostras. English

Sea Tre mallow. Westminster Gar-

den, Mer[rett].

=*Lavatera arborea*, L.

Marrubium folijs tenuius dissectis.

Westminster Garden, R. Cat. pl. =*Lycopus eurofæus*, L.

pp. 183 and 185.

Under a heading: "In my journey [16]77", in a list of plants found in Kent, etc. :—

p. 183.

Turncaps called by Edw. Morgan

Martagon si[ve], see itt

=*Lilium Martagon*, L.

p. 185.

Abrotamnum campestrum. Westmin-

ster garden.

=*Artemisia Abrotamnum*, L.

Brassica marina monospermus. Ibid. =*Crambe maritima*, L.

Brassica siliquosa sempervirens. Ibid. =*Brassica oleracea*, L. ?

Lysimachia lutea fl. globoso. Morgan's

garden

=*Ænothera biennis*, L.

Calendula prolifera

=*Calendula officinalis*, L. var. *prolifera*.

p. 229. This is headed :—

"The following plants among many others I observed in Westminster garden. Anno Dom. 1677."

Acetosa sive opalis ffranca seu Romana =*Rumex scutatus*, L.

Acorus verus offic. Sweet smelling flag. =*Acorus Calamus*, L., var. *verus*, L.

Acorus palustris. Yellow water flag. =*Iris Pseudacorus*, L.

Amygdalus nana indica =*Prunus nana*, L.

Artemisia variegata

=*Artemisia vulgaris*, L. with variegated leaves.

Liliasphodelus phoeniceus : golden day

Lilly

=*Hemerocallis fulva*, L.

Bardana lanuginosis capitulis : woolly

headed burdock.

=*Arctium Lappa*, L. var. *β. tomentosum*, Miller.

Bardana minor

=*Xanthium Strumarium*, L.

Betonica major Danica

=*Stachys officinalis*, Franchet.

Blitum polyspermon

=*Chenopodium polyspermum*, L.

Chamæleon niger

=*Carthamus corymbosus*, L. ?

Carduus mariæ maculatus

=*Carduus Marianus*, L.

Cardamus sive Cnicus : bastard saffron

=*Carthamus tinctorius*, L.

Coriandrum vulgare

=*Coriandrum sativum*, L.

Draba lutea Tetrapetalo siliquis strictis-

simis : arabian mustard

=*Sisymbrium strictissimum*, L.

Cucumis sylvestris

=*Momordica Elaterium*, L.

ffraxinella

=*Dictamnus albus*, L.

Doronicum romanum fl. luteo corim-

bifero

=*Doronicum Pardalianches*, L.

Erysimum alterum Matthioli

=*Turritis hispida*, L. ?

Alnus nigra baccifera

=*Rhamnus Frangula*, L.

Glaux vulgaris Liquorice veterum

=*Glaux maritima*, L.

pishamin virginianum park, Th. : virg.

date plumm or pistamin	= <i>Diospyros virginiana</i> , L.
Gratiola	= <i>Gratiola officinalis</i> , L.
mercurialis mas	= <i>Mercurialis annua</i> , L. ♂.
mercurialis foemina	= <i>Mercurialis annua</i> , L. ♀.
Herniaria	= <i>Herniaria glabra</i> , L.
Isatis fl. luteo	= <i>Isatis Iris</i> , L. ?
Aristolochia clematidis : climbing or running birthwort	= <i>Aristolochia Clematidis</i> , L.

p. 230.

Linaria moravia fl. albo	= <i>Antirrhinum bipunctatum</i> , L., white flowered form ?
Morus nigra	= <i>Morus nigra</i> , L.
Lysimachia cœrulea spicata	= <i>Veronica maritima</i> , L.
Nasturtium Barbareæ facie	= <i>Arabis Halleri</i> , L.
Oleaster Bohemica	= <i>Elæagnus angustifolius</i> , L.
Ononis fl. albo	= <i>Ononis spinosa</i> , L., white flowered var.
Panax Heracleum majus : Hercules great Allheale flosculis luteis.	= <i>Opopanax Chironium</i> , Koch.
pentaphyllum erectum	= <i>Potentilla rupestris</i> , L., <i>P. fruticosa</i> , L. or <i>P. erecta</i> (L), Hampe.
pseudanum majus	= <i>Peucedanum officinale</i> , L.
Pinus	= <i>Pinus Pineæ</i> , L. ?
Pinaster	= <i>Pinus Pinaster</i> , L.
Prunella fl. albo	= <i>Prunella laciniata</i> , L.
Rubia tinctorum	= <i>Rubia tinctorum</i> , L.
Caucalis hispanica	= <i>Tordylium peregrinum</i> , L.
Colutea vesicaria	= <i>Colutea arborescens</i> , L.
Thapsia carote facie : scorching ffennell	= <i>Thapsia fetida</i> , L.
Tithymalus creticus lunatus minor Morisoni	= <i>Euphorbia</i> sp.
Linaria panonica sempervirens spicata	= <i>Antirrhinum genistifolium</i> , L.
Verbena urticæ folio	= <i>Verbena urticifolia</i> , L. ?
Vitis laciniata	= <i>Vitis vinifera</i> , L.
Rhus Corariorum	= <i>Rhus Coriaria</i> , L.
Phalaris	= <i>Phalaris canariensis</i> , L.
Asclepias fl. albo pentapetalo	= <i>Vincetoxicum officinale</i> , Moench.

p. 231.

Nasturtium indicum	= <i>Tropæolum minus</i> L., and <i>T. majus</i> , L.
Malus granata Balaustica : pomgranat.	= <i>Punica granatum</i> , L., double flowered var.
Crithmum chrysanthemum	= <i>Inula crithmoides</i> , L.
Bellis tanacetifolio	= <i>Chrysanthemum corymbosum</i> , L.
Chamælæa tricoccos : Widdow waile flo. luteo triphylo	= <i>Cneorum tricoccos</i> , L.
[Trifolium fruticans Johnson, luteum triphyllon (erased)]	= <i>Jasminum fruticans</i> , L.
Centaurea majus Cinaræ folio	= <i>Cnicus centauroides</i> , L.
Althæa fruticosa	= <i>Lavatera Olbia</i> , L.
Scabiosa austriaca	= <i>Scabiosa grumuntia</i> , L.
Laserpitium magnis folijs	= <i>Laserpitium latifolium</i> , L. ?
Laserpitium angustifolium	= <i>Laserpitium angustifolium</i> , L.
paliurus	= <i>Rhamnus Paliurus</i> , L. ?

Yucca sive yucca peruana : Indian

Bread. fl. albis amplis
 Bellis matricariæ folio Morisoni
 Stœcus citrina angustifolia

=*Yucca gloriosa*, L.
 =*Achillea macrophylla*, L.
 =*Helichrysum Stœchus*, L. var. *angustifolium*, DC.
 =*Anagyris fœtida*, L.
 =*Smilax aspera*, L.
 =*Cytisus hirsutus*, L. ?
 =*Laserpitium Siler*, L.
 =*Acanthus mollis*, L.
 =*Aristolochia Clematidis*, L. ?
 =*Aconitum lycoctonum*, L.
 =*Actæa spicata*, L.
 = ?
 =*Cynanchum acutum*, L.
 =*Urtica canadensis*, L.

p. 232.

Campanula rotundifolia alba major
Campanula rotundifolia alba minor

=*Campanula pyramidalis*, L.
 =*Campanula rhomboidalis*, L., var. *lanceolata*, A.DC.

Carthamus Cnicus
Citrus secunda Clusij
Doronicum Americanum Belvidere
Ferula : fennel giant.
Glycyrrhiza echinata
Balsamina femina
Horminum luteum : colis jovis :
Prunella laciniata
Gnaphalium roseum
Lagopus major
Scabiosa centauroides
Melissophyllum Fuchsii
Mentha fl. violaceo
Orobanchia panonica Clusij
Persicaria virginiana
Anagallis fl. albo.

=*Carthamus tinctorius*, L.
 =*Cytisus supinus*, L.
 =*Rudbeckia laciniata*, L.
 =*Ferula communis*, L.
 =*Glycyrrhiza echinata*, L.
 =*Impatiens Balsamina*, L.
 =*Salvia glutinosa*, L.
 =*Prunella laciniata*, L.
 =*Filago pygmæa*, L.
 =*Trifolium arvense*, L.
 =*Scabiosa alpina*, L.
 =*Melittis Melissophyllum*, L.
 =*Mentha* sp. [*M. sylvestris*, L. ?].
 =*Orobanchia vernus*, L.
 =*Polygonum virginianum*, L.
 =*Anagallis arvensis*, L., white flowered var.

Petasites tussilaginis folio.
Petasites folio anguloso fl. albo
Pilosella major

=*Petasites niveus*, Baumgart.
 =*Petasites albus*, Gaertn.
 =*Hieracium Pilosella*, L., *H. dubium*, L. or *H. florentinum*, All.
 =*Tradescantia virginica*, L.
 =*Leucocorydon æstivum*, L. ?
 =*Phyteuma spicatum*, L.
 =*Staphylea pinnata*, L. or *S. trifolia*, L.
 =*Lonicera alpigena*, L.

Phalangium americanum cæruleum
Triphyllum
Rapunculus corniculatus cæruleus
Nux vesicaria
Periclymenum rectum
Periclymenum perfoliatum : Italian
 woodbinde
Rhus virginiana

=*Lonicera Caprifolium*, L.
 =*Rhus typhinum*, L. or *Rh. copallinum*, L.
 =*Rhus Coriaria*, L.
 =*Myrica Gale*, L.
 =*Mentha cervina*, L.
 =*Sedum Telephium*, L. subsp. *S. purpureum*, Link.

Rhus coriaria
Rhus myrtifolia
Pulegium angustifolium
Telephium hispanicum

<i>Thalictrum majus</i>	= <i>Thalictrum majus</i> , Crantz.
<i>Thalictrum minus</i>	= <i>Thalictrum minus</i> , L.
<i>Hedera virg. quinquefolia</i>	= <i>Vitis quinquefolia</i> , L.
<i>Trachelium minus fl. albo.*</i>	= <i>Campanula glomerata</i> , L.
<i>Valeriana marina fl. albo.</i>	= <i>Centranthus ruber</i> , L. var. <i>alba</i> .
<i>Alcea pentaphylla</i>	= <i>Malva moschata</i> , L. ?
<i>Chrysanthemum virg. Morisoni</i>	= <i>Helianthus</i> sp. ?
<i>Lutea cretica, park. aut Cannabis lutea sterilis Contareni</i>	= <i>Datisca cannabina</i> , L.
<i>jacea lutea major capite spinosa</i>	= <i>Centaurea collina</i> , L. var. <i>macrantha</i> D.C. ?
<i>Clematis peregrina cærulea fl. simplicii tetraphyllo: single blew Ladies bower</i>	= <i>Clematis Viticella</i> , L. var.
<i>Cl. peregrina fl. rubro simplicitate tetraphyllo.</i>	= <i>Clematis Viticella</i> , L. var.
<i>Nux vesicaria virginiana trifolia</i>	= <i>Staphylea trifolia</i> , L.
<i>Clematis virginiana hederæfolio: a roundish large leafe</i>	= <i>Menispermum canadense</i> , L.
<i>Libanotis aquilegiæ folio.</i>	= <i>Laserpitium trilobum</i> , L.
<i>Tanacetum crispum</i>	= <i>Tanacetum vulgare</i> , L. var. <i>crispum</i> , D.C.
<i>Lysimachia lutea globosa</i>	= <i>Lysimachia myrtiflora</i> , L.
<i>Linaria aurea Tragi</i>	= <i>Chrysocoma Linosyris</i> , L.
<i>Sambucus fol. laciniatis</i>	= <i>Sambucus nigra</i> , L. var. <i>laciniata</i> .
<i>Clem. virg. aut flammula Jovis surrecta fl. albo tetrapetalo: virginian Ladies bower</i>	= <i>Clematis virginiana</i> , L.
<i>Sambucus fol. lacinatis</i>	= <i>Sambucus nigra</i> , L. var. <i>laciniata</i> .
<i>Cistus mas folio oblongo incarno.</i>	= <i>Cistus polymorphus</i> , Willk. ?
<i>Sambucus rosea</i>	= <i>Viburnum Opulus</i> , L. var. <i>β. rosea</i> , L.
<i>* Aconitum maximum comam nutante</i>	= <i>Aconitum nutans</i> , L. ?
<i>Cacalia americana</i>	= <i>Eupatorium Ageratoides</i> , L.
<i>Matricaria fl. pleno albo</i>	= <i>Matricaria Parthenium</i> , L. fl. <i>pl.</i>
<i>Eupatorium cannabinum americanum latifolium parkinsoni*: Broad leaved hemplike agrymony of America</i>	= ?
<i>Eupatorium salviæ foliis morisoni</i>	= <i>Eupatorium cannabinum</i> , L. ?
<i>Syringa fl. albo</i>	= <i>Philadelphus coronarius</i> , L.
<i>Cornus mas</i>	= <i>Cornus Mas</i> , L.

* *Cursus secundus.*

p. 234.

<i>Rhamnus catharticus major</i>	= <i>Rhamnus catharticus</i> , L.
<i>Rhamnus catharticus minor</i>	= <i>Rhamnus insectorius</i> , L.
<i>Endivia crispa</i>	= <i>Lactuca sativa</i> , L. var. <i>crispa</i> , L.
<i>Blitum rubrum</i>	= <i>Amaranthus viridis</i> , L.
<i>Lactuca lusitanica</i>	= <i>Lactuca sativa</i> , L. var. <i>crispa</i> , L.
<i>Echium pullo flore</i>	= <i>Lycopsis vesicaria</i> , L.
<i>Lysimachia virginiana lutea angustifolia</i>	= <i>Oenothera biennis</i> , L.
<i>Blattaria fl. luteo amplo</i>	= <i>Verbascum virgatum</i> , Stokes.
<i>Smirnum creticum: Candy Alexander</i>	= <i>Smyrnum perfoliatum</i> , L.
<i>Agrimonia odorata</i>	= <i>Agrimonia Eupatoria</i> , L.
<i>* Teucrium</i>	= <i>Teucrium Polium</i> , L.

* <i>Elatine folio acuminato</i>	= <i>Linaria Elatine</i> , Mill.
<i>Elatine folio subrotundo</i>	= <i>Linaria spuria</i> , Mill.
<i>Essula exigua</i> Tragi. <i>Tithymalus leptophyllus</i> .	= <i>Euphorbia exigua</i> , L.
<i>Chamædrys multifida</i>	= <i>Teucrium spinosum</i> , L. ?
<i>Apocynum aut periploca repens angustifolia flore fusco pentapetalo subtus herbaceo</i>	= <i>Periploca græca</i> , L. ?
<i>Heliotropium flos albis pentapetalis</i>	= ?
<i>Bupthalmum foliis millefoliis luteum</i> Gerrhard	= <i>Anacyclus valentinus</i> , L.
<i>trifolium fruticosum</i>	= <i>Jasminum fruticosum</i> , L.
<i>Asclepias fl. nigro pentapetalo</i>	= <i>Vincetoxicum nigrum</i> , Moench.
<i>Cichoreum album caule alato</i>	= <i>Cichorium Intybus</i> , L. f. <i>sativum</i> , white flowered var.
<i>Scolymus luteus</i>	= <i>Scolymus hispanicus</i> , L.
<i>Verbena supina</i> Clusij	= <i>Verbena supina</i> , L.
<i>Vermicularis</i>	= ?
<i>Branca ursina spinosa</i>	= <i>Acanthus spinosissimus</i> , L.
<i>Abrotamnum viridum rosmarinifolio</i>	= <i>Santolina rosmarinifolia</i> , L. var. <i>vulgaris</i> (Boiss), Willk. et Lange.
<i>Abr. ericæ folio</i>	= <i>Santolina rosmarinifolia</i> , L. ?
<i>Unguentularia</i>	= <i>Santolina Chamæcyparissus</i> , L.
<i>Arbor Judas</i>	= <i>Cercis Siliquastrum</i> , L.
<i>Oleander fl.</i> { <i>albo</i>	= <i>Nerium Oleander</i> , L. var. <i>album</i> and
<i>Luteo</i>	<i>N. Oleander</i> , L. var. <i>luteum</i> .
<i>Cytisus hispanica vel spicata</i>	= <i>Cytisus nigricans</i> , L.

p. 235.

<i>Hippoglossum</i>	= <i>Ruscus Hypoglossum</i> , L.
<i>Lychnis hirta fl. eleganter variegata</i>	= <i>Silene quinquevulnera</i> , L.
<i>flos cardinalis</i>	= <i>Ipomœa Quamoclit</i> , L.
<i>Halymus arborescens</i>	= <i>Atriplex Halimus</i> , L.
<i>Hyacinthus peruanus</i>	= <i>Scilla peruviana</i> , L.
<i>Hypericum frutescens</i>	= <i>Spirœa hypericifolia</i> , L.
<i>Parmica Imperati</i>	= <i>Xeranthemum annuum</i> , L.
<i>Lychnis frutescens myrtifolia</i>	= <i>Silene fruticosa</i> , L.
<i>Lychnis noctiflora</i>	= <i>Silene noctiflora</i> , L.
<i>Genista Hispanica</i>	= <i>Spartium junceum</i> , L.
<i>Cardiaca crispa</i>	= <i>Leonurus Cardiaca</i> , L. ?
<i>Viola mariana purpurea</i>	= <i>Campanula medium</i> , L.
<i>Chelidonium quercij foliis (s) botroides</i>	= <i>Chelidonium majus</i> , L.
<i>Blattaria petulis curtis</i>	= <i>Verbascum</i> , sp. ?
<i>Chæmamolum nudum</i> : sweet naked si[ve]	= a rayless form of <i>Matricaria Parthenium</i> , L.
<i>Trachelium fl. albo.</i>	= <i>Campanula glomerata</i> , L.
<i>Stoebe argentea major</i>	= <i>Centaurea splendens</i> , L.
<i>Thlaspi creticum variegatum</i> : Tufted mustard	= <i>Iberis umbellata</i> , L. ?
<i>Matricaria umbone fistuloso</i>	= a rayless form of <i>Matricaria Parthenium</i> , L.
<i>Matricaria bullatis fl.</i> : naked feverfew	= a form of <i>Chrysanthemum Parthenium</i> Bernh.
<i>Stoebe persica</i> . Knapweed, hoary broad lacinated leaves	= ?

Pyracantha	= <i>Mespilus Pyracantha</i> , L.
Lotus arbor	= <i>Celtis australis</i> , L.
Scordium	= <i>Teucrium Scordium</i> , L.
Sedum rosaceum morisoni aut Sedum Alpinum crenatum asperum Bauhini	= <i>Saxifraga aspera</i> , L.
Hesperis sive viola matronalis fl. rubro pleno.	= <i>Hesperis matronalis</i> , L. fl. pl.
Anagallis terrestris fl. albo	= <i>Anagallis arvensis</i> , L. white flowered var.
Cepea Matthioli fl. albo pentapetalo	= <i>Allium Ascalonicum</i> , L.
Leucocum annuum elegans [album (erased)]	= <i>Cheiranthus annuus</i> , L.
Cotula consolida fl. pleno.	= <i>Delphinium Consolida</i> , L. ?
Coriandrum	= <i>Coriandrum sativum</i> , L.
Oleaster bohemicus cappadocidæ	= <i>Elæagnus angustifolia</i> , L.

* Cursus tertius.

p. 236.

Eryngium montanum fl. cæruleo.	= <i>Eryngium amethystinum</i> , L. ?
Caryophyllus : Deptford Pink	= <i>Dianthus Armeria</i> , L.
Chrysanthemum salicis folio ramosum	= ?
Horminum	= <i>Salvia Horminum</i> , L.
Lactuca lusitanica Aethiopica	= <i>Lactuca</i> , sp. ?
fferulago	= <i>Ferulago communis</i> , L., or <i>F. glauca</i> , L.
Myagrum semine rotunda	= <i>Myagrum paniculatum</i> , L.
Eryngium mediterraneum	= <i>Eryngium campestre</i> , L.
Lactuca sylv. foliis non dissectis costa spinosâ	= <i>Lactuca Serriola</i> , L.
Calamintha spicata	= <i>Saturia</i> , sp. ?
* Geranium bohemicum fl. cæruleo	= <i>Geranium bohemicum</i> , L. ?
* Eruca siliqua quadrangula echinata	= <i>Bunias Eruca</i> , L.
Cachrys peucedani folio semine sulcato minor	= <i>Cachrys Libanotis</i> , L.
Lotus cretica argentea	= <i>Lotus creticus</i> , L.
Psyllium foliis crenatis	= <i>Plantago afra</i> , L.
Thapsicum	= (would this be <i>Thapsia foetida</i> , L. ?).

* Cursus quartus in ye cross passage.

Scabiosa judica	= a <i>proliferous form of Scabiosa maritima</i> , L. var. <i>atropurpurea</i> , L. ?
pomum Amoris	= <i>Lycopersicum esculentum</i> , L.
Papaver corniculatum luteum	= <i>Glaucium flavum</i> , Crantz.
Senecio acris alba fl. herbaceo	= ?
Lychnis myrtifolia frutescens fl. penta- petalis profundi divis	= <i>Silene fruticosa</i> , L.
* Lychnis noctiflora	= <i>Silene noctiflora</i> , L.
Chamælina	= <i>Linum catharticum</i> , L. ?
Aegilops narbonensis Lobelij : french Haver grass	= <i>Aegilops ovata</i> , L.
Tragopogon Luteum minus	= <i>Tragopogon pratensis</i> , L.
Eryngium mediterraneum sive cam- pestre	= <i>Eryngium campestre</i> , L.

p. 237.

Coniza odorata	= <i>Erigeron acre</i> , L. ?
* <i>Alsine bacciflora</i>	= <i>Cucubalus baccifer</i> , L. ?
Horminum fl. albo.	= <i>Salvia Horminum</i> , L. white flowered variety.
Scabiosa centauroides	= <i>Scabiosa alpina</i> , L.
Cynaris hispanica	= <i>Cynara</i> sp. [<i>C. humilis</i> , L. ?].
* <i>Brassica marina</i> siliquosa semper-virens	= <i>Brassica oleracea</i> , L. ?
<i>Brassica marina</i> monospermos	= <i>Crambe maritima</i> , L.
<i>Muscipula</i> fl. rubro	= <i>Silene Muscipula</i> , L. var. ?
<i>Chrysanthemum salicis</i> folio ramosum	= ?
<i>Cnicus tingitana</i>	= <i>Centaurea tingitana</i> , L. ?
<i>Jesminum luteum</i> bacciferum, Bauhini	= <i>Jasminum fruticans</i> , L.
<i>Cistus mas</i> fl. albo.	= <i>Cistus incanus</i> , L.
<i>Hedysarum clypeatum</i> fl. albo	= <i>Hedysarum coronarium</i> , L. var. album.
<i>Horminum Tingitanum</i> folijs dissectis obscure virentibus	= <i>Salvia tingitana</i> , L.
<i>Cyanus amaras</i>	= <i>Centaurea amara</i> , L. ?
<i>Eryngium mediterraneum</i>	= <i>Eryngium campestre</i> , L.
<i>Eryngium marinum</i>	= <i>Eryngium maritimum</i> , L.
<i>Chamæleon niger</i>	= <i>Carthamus corymbosus</i> , L.
<i>Atractilis Tingitana</i>	= <i>Carthamus tingitanus</i> , L.
<i>Moly Homericum</i>	= <i>Allium Moly</i> , L.
* <i>Papaver spinosum</i>	= <i>Argemone mexicana</i> , L.

* *Cursus quintus*.

<i>Martagon pomponium</i> folijs dense confertis	= <i>Lilium pomponium</i> , L. ?
<i>Ornithogalum spicatum</i> album	= <i>Ornithogalum latifolium</i> , L. or <i>O. narbonensis</i> , L.
<i>Arbor Tingitana virginiana</i>	(is this <i>Rhus Toxicodendron</i> , L. ?).
<i>Agaricus castus</i>	= ?
* <i>Digitalis ferruginea latifolia</i>	= <i>Digitalis ferruginea</i> , L.

p. 238.

<i>Sideritis scoridioides</i> Lobelij	= <i>Sideritis Scordiodides</i> , L.
<i>Lactuca arabica</i>	= (cannot be identified).
<i>Chrysanthemum creticum</i> fl. molino	= a form of <i>Chrysanthemum coronarium</i> , L. ?
<i>Herba Doriæ</i> Lobelij	= <i>Senecio Doria</i> , L.
<i>Herba Doriæ altera</i>	= <i>Senecio sarracenicus</i> , L.
<i>Veronica supina</i>	= <i>Veronica Teucrium</i> , L.
<i>Lactuca lusitanica</i>	= <i>Lactuca sativa</i> , L. var. <i>crispa</i> , L.
<i>Mercurialis mas.</i>	= <i>Mercurialis annua</i> , L. ♂.
<i>Mercurialis femina</i>	= <i>Mercurialis annua</i> , L. ♀.
<i>Calendula prolifera</i>	= <i>Calendula officinalis</i> , L. var. <i>prolifera</i> .
<i>Atriplex hortensis rubra</i>	= <i>Atriplex hortensis</i> , L. var. <i>rubra</i> .

Cursus sextus, beginning at the Arbour to ye other end of the garden, and so back through ye middle walk.

<i>Amygdalus</i>	= <i>Prunus Amygdalus</i> , L.
<i>Morus nigra</i>	= <i>Morus nigra</i> , L.
<i>Pistamin virginianum parkinsoni</i>	= <i>Diospyros virginiana</i> , L.

Rhamnus salicis folio	= <i>Hippophaë Rhamnoides</i> , L.
Senecio acris alba	= ?
Sideritis fl. albo	= <i>Stachys annua</i> , L. ?
Virgaurea limonii folio.	= [see notes on Edward Morgan's plants in Herb. Sloane, Vol. 83, below].
Herba Doriæ	= <i>Senecio Doria</i> , L.
Herba Doriæ alba	= <i>Senecio Doria</i> , L. white flowered variety.
Lychnis hir[su]ta minor fl. albo.	= <i>Silene quinquevulnera</i> , L.
Scammonia monspeliaci affinis acutiori folio.	= <i>Cynanchum acutum</i> , L.
Juniperus major	= <i>Juniperus Oxycedrus</i> , L. ? or <i>J. phænicea</i> , L.
Halimus arborescens	= <i>Atriplex Halimus</i> , L.
Tapsus barbatus fl. ocri luteo	= <i>Verbascum Thapsus</i> , L. ?
Abrotona tria	= <i>Santolina Chamæcyparissus</i> , L. var. <i>villosa</i> , Mill.

p. 239.

Lamium album parietariæ facie Novæ Angliæ	= <i>Lamium album</i> , L. var. <i>integrifolium</i> Nolte ex Sonder.
Morus alba	= <i>Morus alba</i> , L.
Cirsium Britannicum repens Clusij	= <i>Carduus helenoides</i> , L.

Cursus septimus.

Lilium bulbiferum	= <i>Lilium bulbiferum</i> , L.
Asclepias fl. nigro pentapetalo	= <i>Vincetoxicum nigrum</i> , Moench. ?
Aster luteus virginianus caule membranaceo	= <i>Aster</i> sp. ?
Aster virginianus latifolius luteus repens	= <i>Aster puniceus</i> , L. ?
Asphodelus albus non ramosus	= <i>Asphodeline lutea</i> , Reichb.
Apocynum rectum latifolium americanum	= <i>Philibertia clausa</i> , K. Schum.
Barba Capre floribus oblongis v. lunaria peregrina, Clusij.	= <i>Spiræa Aruncus</i> , L.
Lamium panonicum rotundifolium	= <i>Lamium Orvala</i> , L.
Angelica lucida canadensis Cornuti (erased : but the name occurs below almost immediately).	= <i>Angelica lucida</i> , L.
fragaria ponte phylloides Morisoni : this hath a strawberry leafe and Cinkfoil flowers.	= <i>Potentilla rupestris</i> , L.
Angelica lucida canadensis Cornuti	= <i>Angelica lucida</i> , L.
Lactuca Arabica.	= (cannot be identified.)
* Draba lutea siliquis strictissimis Camerarij	= <i>Sisymbrium strictissimum</i> , L.
Asclepias fl. albo.	= <i>Vincetoxicum officinale</i> , Moench.
Cymbalaria italica : Bastard Navelwort.	= <i>Linaria Cymbalaria</i> , L.
Amini by the pot Agnus Castus.	= <i>Ammi majus</i> , L. and <i>Vitex Agnus Castus</i> , L.
Mentastrum tuberosa radicum	= <i>Nepeta tuberosa</i> , L.
Calamintha montana præstantior	= <i>Thymus Serpyllum</i> , L. ?
Anagallis cærulea pentapetala	= <i>Anagallis linifolia</i> , L.
Stoebe salamanti	= <i>Centaurea salamantica</i> , L.

Geranium Batræoides fl. albo variegato=*Geranium sylvaticum*, L. white
flowered form.

Chamæmespilus =*Mespilus Cotoneaster*, L.

p. 240.

Prunella fol. dissectis fl. cæruleo. =*Prunella* sp. (a hybrid *P. grandiflora* ×
P. laciniata ?).

Gramen plumosum =*Calamagrostis Epigeios*, Roth. vel.
Stipa pinnata, L.

Smyrniurn creticum =*Smyrniurn rotundifolium*, Mill.

Aster salicis folio =*Bupthalmum salicifolium*, L.

Liliasphodelus minor luteus : yellow
day Lilly. =*Hemerocallis fulva*, L.

Scrophularia lutea =*Schrophularia vernalis*, L. ?

Platanus occidentalis =*Platanus occidentalis*, L.

Platanus orientalis, ye more Cutt. =*Platanus orientalis*, L.

Eupatorium cannabinum mas =*Eupatorium cannabinum*, L. ?

Antirrhinum minus fl. albo =*Antirrhinum Orontium*, L. white
flowered var. ?

Stramonium =*Datura Stramonium*, L.

Lathyrus Tingitana fl. amplo purpureo
siliquis =*Lathyrus tingitanus*, L.

Nigella napa Brassica = (is this *Nigella salvia*, L. ?).

Viola mariana fl. cæruleo =*Campanula mollis*, L.

Bellis Tannacetifolio =*Chrysanthemum corymbosum*, L.

Aphaca =*Lathyrus Aphaca*, L.

Trachelium in maritimis Lobelij. =*Campanula rapunculoides*, L.

Acorus verus (s) Calamus Aromaticus =*Acorus Calamus*, L. var. *verus*, Mill.

Eruca siliqua hirsuta. Eruca mon-
speliacea siliqua quadrata echinata
fl. luteo tetrapetalo =*Bunias Erucago*, L.

p. 241. Cursus octavus beginning on $\bar{y}$ west corner and go round
about that division.

Scabiosa centauroides =*Cephalaria alpina*, Schrader ?

Papaver rheas fl. pleno =*Papaver rheas*, L. var. fl. pl.

Trifolium stellatum in a pott. =*Trifolium stellatum*, L.

Apocynum syriacum umbelliferum
Cornuti =*Asclepias syriacus*, L.

Cachrys peucedani folio in $\bar{y}$ pott. = ?

Menastrum panonicum Clusij =*Nepeta pannonica*, L.

Bardana lanuginosis capitulis =*Arctium Lappa*, L. var. *tomentosa*, L.

Branca ursina =*Acanthus mollis*, L.

Capparis fabago =*Zygophyllum Fabago*, L.

Ageratum fl. luteo =*Achillea Ageratum*, L. ?

Chamæpitys =*Teucrium Chamæpitys*, L.

ptarmica Imperati =*Xeranthemum annuum*, L.

cotula non foetida fl. pleno =*Matricaria inodora*, L. var. fl. pl.

panax Heracleum majus sphondilij
folio =*Opopanax Chironium*, L. or *O. hispi-*
dum, Griseb.

Jacea lutea minor capite spinoso. =*Centaurea collina*, L. var. *macrantha*,
D.C.

Abrotamnum campestre inodorum =*Artemisia crithmifolia*, L.

Lepidium annuum =*Cochlearia glastifolia*, L. or *Lepidium*
petreum, L.

Chondrilla species	= <i>Chondrilla</i> sp. ? or <i>Lactuca</i> sp. ?
Melissa italica hirsuta	= <i>Melissa officinalis</i> , L.
Chamæcissa : on y ^o 1st mannured bed.	= <i>Euphorbia maculata</i> , L. ?
Ocimum	= <i>Ocimum Basilicum</i> , L.
Linaria æstiva fl. amplo.	= <i>Helianthemum</i> sp.
palma Xsti	= <i>Ricinus communis</i> , L.
stramonium	= <i>Datura Stramonium</i> , L.
capsicum	= <i>Capsicum annuum</i> , L.
plantago lagopoides	= <i>Plantago Lagopus</i> , L. ?
Anthyllis maritima lentifolia	= <i>Arenaria peploides</i> , L.
Coriandrum ramosum ex Aleppo	= ?
Myagrum semine rotundo	= <i>Myagrum paniculatum</i> , L. ?
Scabiosa hispanica 2 ^{da} Clusij	= <i>Scabiosa stellata</i> , L.
Thymus creticum capitatum	= <i>Satureia capitata</i> , L. ?
Alcea vesicaria capitis bonæ spei	= <i>Hibiscus Trionum</i> , L. perhaps the var. <i>vesicarius</i> , Cav.
All those on that bed. [=32 plants.]	

p. 242.	then take in all ye parts on y ^e side of the division.
Glastum	= <i>Isatis tinctoria</i> , L.
Yucca, yucca.	= <i>Yucca gloriosa</i> , L.
Lotus Libica Dalescampij hirsuta	= <i>Lotus erectus</i> , L. ?
* Carduus globosus lanceolatus	= <i>Echinops sphaerocephalus</i> , L. ?
Reseda cantabrica	= ?
Digitalis fl. albo	= <i>Digitalis purpurea</i> , L. white flowered variety.
Nux juglans nigra virginiana	= <i>Juglans nigra</i> , L.
Jesminum persicum	= <i>Syringa persicum</i> , L.
Scam[m]onium verum	= <i>Convolvulus Scammonium</i> , L. ?
Ænanthe angustifolia	= <i>Ænanthe silaifolia</i> , Bieb. ?
Lysimachia purpurea spicata folijs sub- rotundis	= <i>Lythrum Salicaria</i> , L.
Atriplex foetida	= <i>Chenopodium Vulvaria</i> , L.
* Beta cretica aculeata	= <i>Emex spinosa</i> , Campd.
* Acetosa vesicaria	= <i>Rumex tingitanus</i> , L. ?
Stramonium crassis et languioribus spinis.	= <i>Datura ferox</i> , L.
Carduus Leucographia capite minori	= a form of <i>Carduus Leucographus</i> , L. ?
Urtica Romana	= <i>Urtica pilulifera</i> , L.
Scolymus luteus	= <i>Scolymus hispanicus</i> , L. ?
Melissa turcica fl. cæruleo by it is.	= <i>Dracocephalum Moldavica</i> , L.
ffumaria tenuifolia fructa compresso	= <i>Fumaria spicata</i> , L. ?
Lini, Morison.	= <i>Portulaca oleracea</i> , L. ?
portulaca folio lutescente	= <i>Physalis pubescens</i> , L. ?
Alkakangi virginianum	= <i>Hedysarum coronarium</i> , L.
Hedysarum clypeatum	= <i>Argemone mexicana</i> , L.
papaver spinosum	= <i>Linum usitatissimum</i> , L.
Linum humilis fl. majore	= <i>Echium creticum</i> , L.
Echium creticum majus	= ?
Echium Tingitanum variegatum	= ?
Chrysanthemum africanum fl. nudo	= <i>Tagetes</i> sp.
capite cernuo Morison	
p. 243.	
Carduus lacteus syriacus fl. albo.	= <i>Cirsium syriacum</i> , Gaertn.

- Botrys aut Atriplex odorata = *Chenopodium Botrys*, L.
 Anagallis fl. albo. = *Anagallis arvensis*, L. white flowered
 var.
 Anthyllis vesicaria hispanica = *Anthyllis tetraphylla*, L.
 ———second part of the garden divided
 by the over thwart way.——
 Althæa fruticosa = *Lavatera Olbia*, L.
 Rhamnus salicis folio = *Hippophaë rhamnoides*, L.
 Absinthium maritimum Lavendulæ
 folia = *Artemisia cærulescens*, L.
 Thlaspi incanum mechliniense of
 mehlen = *Alyssum incanum*, L.
 Ammi quorundam Dalechampi.
 Eryngium quartum Dodonæi. eryn.
 serratifolia Bauhini = *Sium Falcaria*, L.
 Saponaria convoluto folio = *Saponaria officinalis*, L. var. hybrida,
 L. ?
 Dentaria Rondoletij = *Plumbago europæa*, L.
 Agrifolium variegatum = *Ilex Aquifolium*, L. var. variegatum.
 Cardiaca fol. eleganter crispis = *Leonurus Cardiaca*, L. ?
 Hieracium Leptomacron caulon = *Crepis pulchra*, L. or *Hieracium*
 murorum, L.
 Castanea equina = *Æsculus Hippocastanum*, L.
 Lappathum spinosum = *Rumex spinosus*, L. ?
 Nasturtium barbareæ facie = *Arabis Halleri*, L.
 Ligustrum variegatum = *Ligustrum vulgare*, L. var. variegatum.
 fferulago Dodonæi = *Ferulago communis*, L. or *F. glauca*, L.
 Scabiosa hispanica 2^{da} Clusij = *Scabiosa stellata*, L.
 Apios Americana Cornuti = *Glycine Apios*, L.
 Mirabile peruanum = *Mirabilis Jalapa*, L.
 Malus granata Balausticum = *Punica granatum*, L. double flowered
 form.
 Psyllium fol. crenatis = *Plantago afra*, L.
 Arbor virginiana euonymi facie phyle-
 dris = *Robinia pseudacacia*, L.
 Amygdalus nana Indica = *Prunus nana*, L.
 p. 244.
 Laurus Alexandrina = *Ruscus Hypophyllum*, L.
 Quercus glande majori, parkins.[on] = *Quercus Cerris*, L.
 Ilex glandifera = *Quercus Ilex*, L.
 phyllerea folio lato serrato = *Phillyrea latifolia*, L.
 phyllurea angustifolia = *Phillyrea angustifolia*, L.
 fflos cardinalis = *Ipomœa Quamoclit*, L.
 Pinus = *Pinus Pineæ*, L. ?
 *Urtica Romana = *Urtica pilulifera*, L.
 *Urtica Romana urticæ vulgaris folio = *Urtica vulgaris*, L.
 Hieracium castorei odoros monspeli-
 sibis si[ve] Westminster garden = *Crepis fetida*, L., *Crepis taraxifolia*
 L. or *Urospermum Dalechampii*,
 F. W. Schmidt.
 Hieracium luteum glabrum sive Apha-
 coides : ibid = *Crepis* sp. ?
 Belvidere sive scoparia græcorum.
 Broom Toad flax. ibid. = *Antirrhinum genistifolium*, L.
 Balsamita = *Chrysanthemum Balsamita*, L. ?

p. 299.

On the right hand, under the wall, grows :

<i>Hedera virginiana</i> quinquefolia	= <i>Vitis quinquefolia</i> , Lam.
<i>Jesminum persicum</i>	= <i>Syringa persica</i> , L.
Herb. Ger. by 3 & 2 P.	= <i>Egopodium Podagraria</i> , L.
<i>Hipposelinum</i>	= <i>Smyrniolum Olusatrum</i> , L.
<i>Seseli æthiopicum</i> : Hartwort	= <i>Bupleurum fruticosum</i> , L.
<i>Scrophularia lutea</i>	= <i>Scrophularia vernalis</i> L.
<i>Stobe poliponesiacum</i>	= <i>Centaurea spinosa</i> , L. ?
dog's bane	= <i>Vinca major</i> , L.
<i>Apolymus repens salicis folio</i> : like a willow	= ?
<i>Flammulo jovis</i> , or <i>Clematis virginiana</i> num	= <i>Clematis Flammula</i> , L. or <i>Menispermum canadense</i> , L.
<i>Trachelium fl. pleno</i>	= <i>Campanula glomerata</i> , L.
<i>Atriplex sativa purpurea</i>	= <i>Atriplex hortensis</i> , L.
<i>Laserpitium latifolium</i> sive <i>peucedanum majus</i>	= <i>Laserpitium latifolium</i> , L.
<i>Clematis peregrina fl. simplicii</i> [peregrina (erased)].	= <i>Clematis Viticella</i> , L. ?
<i>Cacalia Americana</i>	= <i>Eupatorium Ageratoides</i> , L.
<i>Atriplex sativa alba</i>	= <i>Atriplex hortensis</i> , L.
<i>Cyanoglossum sempervirens</i>	= <i>Cyanoglossum montanum</i> , L.
<i>Borrago minor herbariorum</i>	= <i>Omphalodes verna</i> , Moench.
<i>Borrago sempervirens</i>	= <i>Anchusa sempervirens</i> , L.
<i>Blattaria lutea perennis</i>	= <i>Verbascum Blattaria</i> , L. ?
<i>Lutea cretica</i>	= ?
<i>Stachys cretica angustifolia</i>	= <i>Stachys cretica</i> , L. ?
<i>Stachys folio obscure virenti</i>	= <i>Stachys ambigua</i> , Sm. (a hybrid <i>S. palustris</i> × <i>S. ambigua</i>).
<i>Marrubium nigrum longifolium</i>	= <i>Phlomis Herba venti</i> , L.
<i>Ocimum fistulosum Mentastrum polium montanum</i>	= <i>Ocimum Basilicum</i> , L. ?
<i>Thalictrum hispanicum</i>	= <i>Teucrium Polium</i> , L.
<i>Ribes grossulariæ folio</i>	= <i>Thalictrum flavum</i> , L. ?
<i>panax Heraclis</i> by ye <i>Ornus</i>	= <i>Ribes Grossularia</i> , L.
	= <i>Opopanax Chironium</i> , Koch. and <i>Pyrus Aucuparia</i> , L.
<i>Rosa virginiana</i>	= <i>Rosa</i> ? sp.
<i>virga aurea Americana</i>	= <i>Solidago odora</i> , Ait.
<i>petroselinum macedonicum</i>	= <i>Bubon macedonicum</i> , L.
<i>Eupatorium Americanum</i> (erased)	
<i>Conyza alba Americana</i>	= <i>Erigeron canadense</i> , L.
<i>Rhus plinij mirtifolia</i>	= <i>Coriaria myrtifolia</i> , L.
<i>Aster atticus</i>	= <i>Aster amellus</i> , L.
<i>Veronica Teucri facie</i>	= <i>Veronica Teucrium</i> , L.
<i>Carduus globosus</i>	= <i>Echinops sphærocephalus</i> , L.

2. Direct walk on ye right hand.

pseudo <i>Citysus foliis subrotundis</i> aut 2 nd Gerardi	= <i>Cytisus sessilifolius</i> , L.
<i>Scabiosa montana magna</i>	= <i>Cephalaria leucantha</i> , Schrad. ?
<i>periclymenum erectum fructu rubro</i>	= <i>Lonicera alpigena</i> , L.
<i>Syringa purpurea</i>	= <i>Syringa vulgaris</i> , L. var. <i>purpurea</i> , Weston.

<i>Nux vesicaria virginiana</i>	= <i>Staphylea trifolia</i> , L.
<i>Carduus pratensis</i>	= <i>Cnicus oleraceus</i> , L.
<i>periclymenum erectum germanicum</i>	= <i>Lonicera Xylosteum</i> , L.
<i>Sambucus racemosa</i>	= <i>Sambucus racemosa</i> , L.
<i>Genista Hispanica</i> : Westminster	= <i>Spartium junceum</i> , L.
<i>Amaranthus elegans</i> : ibid.	= ?
<i>Speculum veneris perfoliatum</i> : ibid.	= <i>Specularia hybrida</i> , DC. ?
<i>Echium creticum variegatum</i> : ibid.	= <i>Echium creticum</i> , L., var.
<i>Colutea vesicaria</i>	= <i>Colutea arborescens</i> , L.
<i>Marrhubium foliis tenuius dissectis</i>	
<i>Tingitanum</i> : ibid.	= <i>Lycopus europæus</i> , L.

Total recorded by Ward, 1677=484 plants.

C. As Recorded by Contemporary Authors or Preserved in Herbaria.

(Ray, 1670.)

Marrubium aquaticum Ger. emac. aquat. vulgare Park. aquat. quorundam
J.B. palustre glabrum C.B.
Water Horehound = *Lycopus europæus*, L.

[This was collected by Thomas Willisel and grown by Edward Morgan.]

(Plukenet, 1672.)

Gramen Phaleroid = *Phalaris paradoxa*, L. ?

(Morison, 1672.)

Cachrys seu Libanotis Cachryophorus = *Cachrys lavigata*, DC. ?

Pastinaca tenuifolia Daucus seu carota = *Daucus Carota*, L.

Thalictrum siliqua striata = *Thalictrum* sp. ?

Thalictrum siliqua triquetra = ?

Caucalis Daucoides Tingitana = *Daucus muricatus*, L.

(Ray, 1686.)

Persicaria frutescens maculosa Virgini-
ana flore albo Park. = *Polygonum virginianum*, L.

Alcea major et procerior : An *Alcea*
amplissimo folio laciniato, J.B. = *Malva Alcea*, L. ?

Solanum lanuginosum hortensi seu
vulgare simile : Hoary Night-Shadow = *Solanum nigrum*, L. [cited P. Miller
(ed. T. Martyn), Gard and Bot.
Dict. Vol. II Pt. II 1807.]

Medica Catalonica elegans Edwardi
Morgani = a leguminous plant [cited L. Plukenet,
Almagestum Botanicum, 1696 p.
244 : H. Boerhaave, *Index alt.*
Pl. II : 36 (1720)].

(Plukenet, 1691 and 1696).

Alcea Cretica flore immaculati candoris
peramplo = *Hibiscus* sp.

Christophoriano arbor aculeata Virgin-
ensis arborescens spinosæ [et syns.]
Arbor spinosa Fraxinii folij Virgini-
ana D. Edward Morgani = *Aralia spinosa*, L.

- Cistus American, Chamænerij folius
lucentibus = ?
- Horminum majus lusitanicum foliis
profundis incis D. Edv. Morgani.
Horminum sylvestre latifolium Tin-
gitanum H. Edin. = ?
- Jacea montana alato caule purpurea ex
singulis capitulorum squamis spinu-
lis plurimis in hemicyclum dispositis
[et syns]. = *Centaurea muricata*, L.
- Limonium (forte) peregrinum folio
solidiori lectura in laciniae varie
dissecto = *Acrostichum pectinatum*, L.
- Pentaphyllum Alpinum minus supinum
foliis tenuioribus altius serratis
glabris cauticulo purpurascens = *Potentilla supina*, L. [cited P. D.
Giseke : Index Linnæanus in Leon-
hardi Plukenetii Opera Botanica :
Hamburg, 1779, p. 11].
- Salix vulgaris rubens C.B.P. succrevit
in Hort. Medico Edv. Morgan ubi
Salicis Belgicæ viminibus rubris
titulonobisprimoinnotuit (Plukenet
1696, p. 327) = *Salix purpurea*, L.
- Scammonia macrorrhizos cretica Park = *Convolvulus sibiricus*, L.
- Tithymalus Caracas radice pyriformi
Moris. Prælud. Bot. 313. . . An
Tithymalus tuberosus Germanicus
C.B.P. 292 = ?

Two other plants grown by Morgan, to which Plukenet refers, need more detailed notice, and the first of these references may be usefully quoted (Plukenet, 1691, t. 42 and 1696, p. 225).

"Liquid-ambari arbor s. Styraciflua Aceris folio, fructu tribuloide (i.e.) pericarpio orbiculari, ex quamplurimis apicibus, coagmentato semen recondens Phytog. tab. 42 [et syns] . . . Aceris odorati Cretici titulo habuit & D. Edw. Morganus rei Herbariæ suo tempore callentissimus : qui in Horto suo Medico apud Westmonasteriense pone Abbatiam jam olim permultos annos hanc arborem enutrivit et revera nec Acer nec Platanus proprie dici potest : Est enim quædam Heteroclitia & sui generis Arbor."

Mr. A. H. G. Alston kindly drew my attention to two specimens in Herb. Sloane, Vol. 159, fol. 203. Two leaves are pasted on to this page. The one on the left is referred to as "Platanoides sive Aurie, per Mr. Dale," and is also referred to as "Acer odoratum Creticum Ed. Morgan". The specimen on the right is labelled : "Ococotcol s. Styrax liquida", and is of the Sugar Maple, *Acer saccharum*, L. Below these specimens appears a long note in the handwriting of James Petiver. This is headed :

"26. Sweet Gum Tree : Lawson 95."

and followed by a list of synonyms. Then occurs this note :—

"This grew many years ago in old Mr. Edw. Morgan's most famous Garden behind the Abbey Wall at Westminster, who then cal'd it ye sweet scented Maple of Candy, since w^{ch} I have for over 20 years past, observed it with y^e Noble Patron of Botany, y^e Bishop of London, where they now call it y^e Styrax liquidæ, or Sweet Gum Tree."

Petiver's note clearly applies to the specimen on the left, named "Acer odoratum creticum Ed. Morgan". This is *Liquidambar styraciflua*, L., and is the species figured by Plukenet, and grown by Morgan at Westminster and by Bishop Compton at Fulham. Another specimen of this species, but not from Morgan's garden, is to be found in the Morisonian Herbarium at Oxford (Vines & Druce, 1914, p. 261).

The second plant is :

Salvia fruticosa, Cisti folio haud incano
floribus purpureis = *Phlomis italica*, L.

[This was grown by Morgan about 1661, and figured thirty years later (Plukenet, 1691, t. 57). A colour plate of it appeared in P. Miller, "Figures of Plants described in the Gardeners' Dictionary" I : 135, t. 202 (1757).]

[Morison, 1699.]

Lamium annum rubrum Parietariæ
foliis = *Lamium purpureum* L. var. *ocymifolium*, Boulger in *J. Bot.* LI : 150-154 (1903).

[Vines & Druce, 1914, p. 149, report a specimen of this plant "ex horto Dom. Edw. Morgan prope coenobium Westmonasteriense plurimis abhinc annis ipsi comparavimus" in the Morisonian Herbarium at Oxford.]

Pseudo-salvia fruticosa purpurea Ver-
basci angustiorioribus foliis rugosis = *Phlomis purpurea*, L.

[Vines & Druce, 1914, p. 151, report a specimen of it in the Morisonian Herbarium at Oxford, and that it was "cultivated in Morgan's garden at Westminster". P. D. Giseke, *Index Linnæanus in Leonhardi Plukenetii Opera Botanica*, 1799, p. 3, identifies Plukenet's figure (Plukenet, 1691, t. 57) as this species. W. Aiton, *Hort. Kew*, 2nd Ed. III : 407 (1811) credits Morgan with growing it. Sir J. E. Smith in his *Spicilegium Botanicum*, Fasc. I, p. 6, t. 7 (1791) pointed out that Linnaeus in *Species Plant*, Ed. 2, 1762 had confused *Phlomis purpurea*, L. Sp. Pl. 1753 with *P. italica*, L. and gives a colour plate of the true *P. purpurea*, L. Thomas Martyn, in his edition of P. Miller, *Gard. and Bot. Dict.*, Vol. II, Pt. II (1807), accepts this view and also credits Morgan with the cultivation of *P. purpurea*, L. Finally, J. C. Loudon, *Arb. et Frut. Brit.* I : 50 (1838), credits Morgan, correctly apparently, with growing both *Phlomis purpurea*, L. and *P. italica*, L.]

Chamæcyse Virginianus, E. Morgan = *Euphorbia maculata*, L.

[Vines & Druce, 1914, p. 139 report a specimen of this in the Morisonian Herbarium at Oxford, but the plant does not seem to be cited by Morison.]

[Herb. Sloane, Vol. 83.]

Preserved in Vol. 83 in the Sloane Herbarium are some plants marked :—

"Several plants from Tangier, Virginia etc., from the garden of Mr. Edward Morgan in Westminster. The plants are named alphabetically, the first beginning at P. and, about the middle, beginning at A. Almost all referred to Mr. Ray. M. M. 17²57."

and in another hand,

"A Collection of plants gathered by D. Plukenet with names wrote by himself. European plants."

The plants so preserved in this volume are :—

fol. 3. *Platanus virginiana* Parkinson.
Occidental Morgani = *Platanus occidentalis*, L.

- fol. 4. *Platanus orientalis* Edw. Morgan = *Platanus orientalis*, L.
- fol. 17. Quinquefol: folijs serratis
Edvardi Morgani = *Potentilla* sp.
- fol. 53: *Scrophularia americana* Ed-
vardi Morgani: (below, in another
hand) *Scorodoniae folio* = ?
- fol. 68: *Solanum verum antiquorum*
Edvard Morgan = ?
- fol. 70: *Solanum surrectum Indicum*
Edvard Morg. (below, in another
hand) *Solanum Halicacabum*,
veterum. Solau Indictū *Stramonia*
fol. = *Solanum Halicacabum*, L.
- fol. 111: *Vicia Lathyroides* Morison.
Vic. siliquis *Orobi* Morgan (below,
in another hand) *Lathyrus annuus*
siliq. *Orob.* = *Lathyrus* sp. ?
- fol. 112: *Vicia tingitana* flore albo
siliqua hirsuta Morg. = *Vicia* sp. ?
- fol. 116 (a) *Virga aurea* Limonij folio
Ed. Morg. [The word Limonij is
overwritten on another]. cf.
Thomas Lawson's Notebook, 1677
supra = *Solidago sempervirens*, L.
- (b) *Virga aurea* Limonij folio
minor Morgan (below, in another
hand) an foliis lævibus non serratus
Robti Morrison in hort. Bless.
[The word Limonij is again over-
written on another.] = *Solidago Virgaurea*, L.
- back of fol. 137. *Ammi Matth*[?] B.
(erased) *Ammi angustifolium*, Morg. =
- fol. 154. *Bellis Tanaceti folio annua* ex
horto Edvard Morgani (in another
hand) *Chamæmal. Hispanica* C.B. = *Chrysanthemum corymbosum*, L.
- back of fol. 176. *Clematis Tetraphyllos*
Americana Morisoni Limonij odoro
E. Morgan = ?
- fol. 202. *Gladiolus floribus uno versu*
dispositis major CB: *Narbonensis*
Obs. and Icon, Lob. "no proven-
ance" = *Gladiolus communis*, L.
- back of fol. 221 (a) *Horminum sativum*
folijs obscure viriduli E. Morg. = ?
- (b) *Horminum Lusitani-*
cum ex hortulo Morgan = ?
- back of fol. 235. *Lathyrus Africanus*
flore amplo purpureo ex horto Ed.
Morg. = ?
- back of fol. 244. *Lotus latifolio* Ameri-
cana Edvard Morgano = ?

back of fol. 250 (a) *Malva Tingitana*
flore minore Morgan = *Malva* sp.
[specimen badly damaged.]

(b) *Malva Tingitana*
ex horto Morgan = *Malva* sp.

back of fol. 255 *Mentastrium Arabicum*
ffolijs incanis Morgan = ?

Though this volume contains a number of other plants grown in the Westminster Physic Garden, only those specifically attributed to Edward Morgan have been extracted for inclusion here. At the end of the volume is a number of unnamed specimens, and the volume is undated.

[Herb. Sloane, Vol. 26.]

fol. 55. *Solanum vulg.* = *Solanum nigrum*, L.

[cited by T. Martyn in P. Miller, *Gard. and Bot. Dict.*, 1807, Vol. II, as being grown by Morgan, though he does not refer to this specimen.]

back of fol. 155. *Solanum esculentum*.

B. pin. *Battata virginiana* G. = *Solanum tuberosum* L.

[Herb. Sloane, Vol. 26, is marked: "Plants gathered at the Physick Garden in Westminster about the year 1687 Vid Vol. I. M. M. 17 $\frac{1}{9}$ 57." The specimens were thus collected at the time when Rusholm was Gardener, so that this specimen of the potato was grown by him. Edward Morgan also grew the potato, a specimen of which occurs in the Morison Herbarium (Salaman & Hawkes, 1949). This specimen in Herb. Sloane has come to notice since the publication of that paper, the authors of which consider that Morgan's plant was grown perhaps in 1672. They ascribe a similar date to a specimen collected by Leonard Plukenet either in a garden at Westminster, or at Horn Hill, Herts. where he had a farm (Woodward, 1909).]

ACKNOWLEDGMENTS.

Assistance in the preparation of this account of the Westminster Physic Garden has been received from several sources, but special thanks are due to Mr. S. Savage for help and advice especially in regard to Thomas Lawson's Notebook, a transcript of which appears by the courtesy of the President and Council of the Linnean Society of London. Mr. A. H. G. Alston kindly gave me facilities to see material in the Sloane Herbarium in the Department of Botany, British Museum (Natural History), while the Librarian of the Medical Society of London granted facilities to study John Ward's "Diary", extracts from which appear by the courtesy of the President and Council of that Society. To the Public Library staffs in the Cities of London and Westminster I am indebted for assistance with contemporary maps and records.

LIST OF WORKS CONSULTED.

- BARRETT, C. R. B. 1905. *The History of the Society of Apothecaries of London*, 87-97.
BRAY, W. n.d. *The Diary and Correspondence of John Evelyn*, 257.
COLES, W. 1657. *Adam in Eden*.
DRUCE, G. C. & VINES, S. H. 1897 and 1919. *An Account of the Herbarium of the University of Oxford*. Pt. I (1897). Pt. II (1919).
GREENE, M. A. E. 1860. *Calendar of State Papers (Dom. Ser.) Charles II: 1660-1661*, 6.
GUNTHER, R. T. 1920. *Gard. Chron.*, **67**, 240.
———. 1922. *Early British Botanists and their Gardens*, 276-298 and 308.
———. 1937. *Early Science in Cambridge*, 348 and 375.
———. 1945. *Early Science in Oxford*, **14**. The Life and Letters of Edward Lhwyd, 55-6, 70 and 74-5.
JACKSON, B. D. 1908. *Dict. Nat. Biogr.*, **10**, 102.
JOHNSON, T. 1641. *Mercurii Botanica pars altera*.
KEW, H. W. & POWELL, H. E. 1932. *Thomas Johnson, Botanist and Royalist*.
LANKESTER [Sir], E. R. 1898. *The Correspondence of John Ray*, 232, 237.

- MERRETT, C. 1667. *Pinax Rerum Britannicum*, 41-2, 75, 92-3, 95 and 98.
 MILLER, P. (ed. MARTYN, T.). 1807. *Gardeners' and Botanists' Dictionary*, 1 and 2.
 MORISON, R. 1672. *Plantarum Umbelliferum*, 1-2, 31-2 and 61.
 —. 1699. *Plantarum Historiæ Universalis Oxoniensis: Pars Tertia*.
 PLUKENET, L. 1691. *Phytographia: Pars 1-4*, tabs. 6, 20, 231, 8, 42, 57, 85, 95 and 106.
 —. 1696. *Almagestum Botanicum*, 13, 85, 98, 105, 115, 193, 224, 285, 327 and 329.
 POWER, SIR D'ARCY. 1917. *Trans. Med. Soc. Lond.*, 40, 1-26.
 —. 1919. *Ann. Med. Hist.*, 2, 109-125.
 —. 1920. *Trans. Med. Soc. Lond.*, 43, 253-284.
 RAVEN, C. E. 1942. *John Ray, Naturalist*, 150.
 —. 1947. *Early English Naturalists from Neckham to Ray*.
 —. 1948. *Proc. Linn. Soc. Lond.*, 160, 3-12.
 RAY, J. 1670. *Catalogus Plantarum Angliæ*, 206.
 —. 1686. *Historia Plantarum*, 1, 183, 605, 672 and 962.
 SALAMAN, R. N. & HAWKES, J. G. 1949. *Proc. Linn. Soc. Lond.*, 161, 71-84.
 SAVAGE, S. 1948. *Proc. Linn. Soc. Lond.*, 160, 55.
 VINES, S. H. & DRUCE, G. C. 1914. *An Account of the Morisonian Herbarium at Oxford*.
 WILKIN, S. 1852. *The Works of Sir Thomas Browne*, 516-518.
 WOODWARD, B. B. 1909. *Dict. Nat. Biogr.*, 15, 1318.

INDEX OF POST-LINNAEAN GENERA.

(Numbers in brackets indicate number of entries on the page.)

- Acacia, 113.
 Acanthus, 112 (4), 116, 118, 122.
 Acer, 127.
 Achillea, 116, 122.
 Aconitum, 116, 117.
 Acorus, 103, 114, 122.
 Acrostichum, 127.
 Actæa, 116.
 Ægilops, 119.
 Ægopodium, 125.
 Æsculus, 124.
 Agrimonia, 116, 117.
 Alisma, 111.
 Allium, 119, 120.
 Alyssum, 124.
 Amaranthus, 117.
 Ammi, 121.
 Anacyclus, 118.
 Anagallis, 116, 119, 121, 124.
 Anagyris, 116.
 Anchusa, 125.
 Angelica, 121 (2).
 Anthemis, 111.
 Anthyllis, 124.
 Antirrhinum, 115 (2), 122, 124.
 Arabis, 115, 124.
 Aralia, 126.
 Arctium, 114, 122.
 Arenaria, 113, 123.
 Argemone, 120, 123.
 Aristolochia, 104, 115, 116.
 Artemisia, 113 (2), 114 (2), 122, 124.
 Asclepias, 122.
 Asphodeline, 121.
 Aster, 121 (2), 125.
 Atriplex, 118, 120, 121, 125 (2).
 Avena, 113 (2).
 Brassica, 114, 120.
 Bubon, 125.
 Bunias, 112.
 Bupleurum, 125.
 Bupthalmum, 122.
 Cachrys, 119, 126.
 Calamagrostis, 122.
 Calendula, 114, 120.
 Campanula, 116 (2), 117, 118 (2), 122 (2), 125.
 Capsicum, 123.
 Carduus, 114, 121, 123.
 Carthamus, 114 (2), 116, 120 (2).
 Celtis, 119.
 Centaurea, 117, 118, 120 (2), 121, 122, 125, 127.
 Centranthus, 117.
 Cephalaria, 122, 125.
 Cercis, 118.
 Cheiranthus, 119.
 Chelidonium, 118.
 Chenopodium, 114, 123, 124.
 Chondrilla, 123.
 Chrysanthemum, 115, 118, 120, 122, 124, 129.
 Chrysocoma, 117.
 Cichoreum, 118.
 Cirsium, 111, 123.
 Cistus, 117, 120.
 Clematis, 117 (3), 125.
 Cneorum, 115.
 Cnicus, 115, 126.
 Cochlearia, 122.
 Colutea, 115, 126.
 Convolvulus, 123, 127.
 Coriandrum, 114, 119.
 Coriaria, 125.
 Cornus, 117.
 Crambe, 114, 120.
 Crepis, 124 (4).
 Cucubalus, 120.
 Cyanoglossum, 125.
 Cynanchum, 116, 121.
 Cynara, 120.
 Cytisus, 116 (2), 118, 125,
 Datisca, 117.
 Datura, 122, 123 (2).
 Daucus, 126 (2).

- Delphinium, 119.
 Dianthus, 119.
 Dictamnus, 114.
 Digitalis, 120, 123.
 Diospyros, 115, 120.
 Doronicum, 114.
 Dracocephalum, 123.
 Echinops, 123, 125.
 Echium, 123, 126.
 Elæagnus, 115, 119.
 Emex, 123.
 Eupatorium, 117 (2), 122.
 Euphorbia, 115, 118, 123, 128.
 Erigeron, 120, 125.
 Eryngium, 119 (3), 120 (2).
 Ferula, 116.
 Ferulago, 119, 124.
 Filago, 116.
 Fumaria, 112, 123.
 Geranium, 119, 122.
 Gladiolus, 113, 129.
 Glaucium, 119.
 Glaux, 113 (2), 114.
 Glycine, 124.
 Glycyrrhiza, 113, 116.
 Gratiola, 115.
 Hedysarum, 120, 123.
 Helianthemum, 123.
 Helianthus, 117.
 Helichrysum, 116.
 Hemerocallis, 114, 122.
 Herniaria, 115.
 Hesperis, 119.
 Hibiscus, 123, 126.
 Hieracium, 116 (3), 124.
 Hippophaë, 121, 124.
 Hottonia, 113.
 Iberis, 118.
 Ilex, 124.
 Impatiens, 102, 111, 116.
 Inula, 115.
 Ipomoea, 118, 124.
 Iris, 114.
 Isatis, 115, 123.
 Jasione, 111.
 Jasminum, 115, 118, 120.
 Juglans, 123.
 Juniperus, 121 (2).
 Lactuca, 117 (2), 119 (2), 120, 123.
 Lamium, 121 (2), 128.
 Laserpitium, 115 (2), 116, 117.
 Lathyrus, 122 (2), 129.
 Lavatera, 111, 114, 115, 124.
 Leonurus, 118, 124.
 Lepidium, 113, 122.
 Leucojum, 116.
 Ligustrum, 124.
 Lilium, 112, 113, 114, 120, 121.
 Linaria, 118 (2), 121.
 Linum, 119, 123.
 Liquidambar
 Lonicera, 116 (2), 125, 126.
 Lotus, 119, 123.
 Lycopersicum, 119.
 Lycopsis, 117.
 Lycopus, 114, 126 (2).
 Lysimachia, 117.
 Lythrum, 123.
 Malva, 111, 117, 126, 130 (2).
 Matricaria, 117, 118 (2), 122.
 Melissa, 123.
 Melittis, 116.
 Menispermum, 117, 125.
 Mentha, 116 (2).
 Mercurialis, 115 (2), 120 (2).
 Mespilus, 112, 119, 122.
 Mirabilis, 124.
 Momordica, 114.
 Morus, 112, 115, 120, 121.
 Myagrum, 119, 123.
 Myrica, 116.
 Nepeta, 121, 122.
 Nerium, 118 (2).
 Nidularia, 112, 113.
 Nigella, 122.
 Ocimum, 123, 125.
 Oenanthe, 123.
 Oenothera, 114, 117.
 Omphalodes, 125.
 Ononis, 115.
 Opopanax, 115, 122 (2), 125.
 Ornithogalum, 120 (2).
 Ornithopus, 112.
 Orobus, 112, 116.
 Pæonia, 112 (2).
 Papaver, 122.
 Periploca, 118.
 Petasites, 116 (2).
 Peucedanum, 115.
 Phalaris, 106, 115, 126.
 Philadelphus, 117.
 Philibertia, 121.
 Phillyrea, 124 (2).
 Phlomis, 125, 128 (2).
 Physalis, 123.
 Phyteuma, 116.
 Pimpinella, 103, 112.
 Pinus, 115 (2), 124.
 Plantago, 119, 123, 124.
 Platanus, 122 (2), 128, 129.
 Plumbago, 124.
 Polygala, 111.
 Polygonum, 116, 126.
 Populus, 112.
 Portulaca, 123.
 Potentilla, 115 (3), 121, 127, 129.
 Primula, 111 (4).
 Prunella, 115, 116, 122.
 Prunus, 114, 120, 124.
 Punica, 115, 124.
 Pyrus, 125.
 Quercus, 112 (2), 124 (2).
 Rhamnus, 114, 115, 117 (2).
 Rhus, 115, 116 (3), 120.
 Ribes, 125.
 Ricinus, 123.
 Robinia, 124.
 Rosa, 125.

- Rubia, 115.
 Rudbeckia, 103, 116.
 Rumex, 114, 123, 124.
 Ruscus, 118, 124.

 Salix, 127.
 Salvia, 116, 119, 120 (2).
 Sambucus, 117 (2), 126.
 Santolina, 118 (3), 121.
 Saponaria, 124.
 Satureia, 119, 123.
 Saxifraga, 112, 119.
 Scabiosa, 115, 116, 119, 120, 123, 124.
 Scilla, 118.
 Scolymus, 118, 123.
 Scrophularia, 122, 125.
 Sedum, 116 (2).
 Senecio, 120 (2), 121 (2).
 Sideritis, 120.
 Silene, 111, 118 (3), 119 (2), 120, 121.
 Sisymbrium, 114, 121.
 Sium, 124.
 Smilax, 112, 116.
 Smyrnium, 117, 122, 125.
 Solanum, 126, 129, 130 (2).
 Solidago, 125, 129 (2).
 Spartium, 112, 113, 118, 126.
 Specularia, 126.
 Spiræa, 118, 121.
 Stachys, 114, 121, 125 (2).
 Staphylea, 116 (2), 117, 126.
 Strycnos, 112.
 Syringa, 123, 125 (2).

 Tagetes, 123.
 Tanacetum, 117.
 Teucrium, 117, 118, 119, 122, 125.
 Thalictrum, 117 (2), 125, 126.
 Thapsia, 112, 115, 119.
 Thymus, 121.
 Tordylium, 115.
 Tradescantia, 116.
 Tragopogon, 119.
 Trifolium, 103, 116, 122.
 Tropæolum, 113 (2), 115 (2).
 Turritis, 114.

 Urospermum, 124.
 Urtica, 116, 123 124 (2).

 Verbascum, 117, 118, 121, 125.
 Verbena, 115.
 Veronica, 115, 120, 125.
 Viburnum, 117.
 Vicia, 129.
 Vinca, 125.
 Vincetoxicum, 115, 121 (2).
 Vitex, 121.
 Vitis, 115, 117, 125.

 Xanthium, 114.
 Xeranthemum, 118, 122.

 Yucca, 116, 123.

 Zizyphus, 113.
 Zygodphyllum, 122.

PROCEEDINGS OF THE GENERAL MEETING HELD 6 March 1952

Dr. B. BARNES, Vice-President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 21 February 1952, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—Professor A. R. Clapham, Mr. R. H. Haskins, Dr. A. J. T. Janse, Dr. C. T. Prime, the Anglo-Swedish Literary Foundation, and Messrs. Chapman & Hall, Ltd.

The VICE-PRESIDENT reported the death of Johannes Gossweiler, Foreign Member.

A Symposium on Photoperiodism was held, which was opened by Dr. P. F. Wareing, Dr. W. W. Schwabe, Dr. O. N. Purvis and Prof. F. G. Gregory, F.R.S.

A general discussion followed, in which the following took part:—Dr. E. M. Delf, Prof. A. J. Audus and Mr. D. J. Carr; Prof. F. G. Gregory and Dr. P. F. Wareing replied.

SOME RECENT EXPERIMENTS BEARING ON THEORIES OF PHOTOPERIODISM

By P. F. WAREING and D. J. CARR.

The inhibition of flowering in short-day plants by a short 'light-break' interposed during the dark period is generally ascribed to the photo-destruction or reconversion of some dark product 'B' (Gregory, 1947). In the experiments of Carr (1952), however, it was found that when plants of *Perilla ocymoides* were exposed to 48-hour cycles which included a 36–40-hour dark period, flowering was inhibited by a 'light-break' only if this was given during the initial hours of darkness or towards the end of the dark period. In comparable experiments with *Xanthium pennsylvanicum* similar effects were observed, although the inhibition was less marked than in *P. ocymoides*. Such experiments are difficult to interpret according to any hypothesis which involves the photo-inactivation of a dark product 'B', for if 'B' is still light-sensitive after some 30–36 hours of darkness it would be destroyed in the photoperiod following a normal dark period and the effects of successive cycles could not be cumulative.

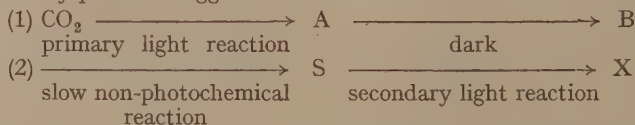
An alternative explanation of these effects is suggested by the hypothesis put forward by Wareing (1950, 1951), to explain the photoperiodic control of the growth of *Pinus sylvestris*. According to this hypothesis the products of the light and dark periods are mutually antagonistic and the formation of the dark product is inhibited during the initial hours of darkness by the carry-over of some substance formed in the preceding light period.

It is now suggested that a secondary light reaction is involved in photoperiodism and results in the formation of a substance 'X' which inhibits the formation of the dark product 'B'. During a main photoperiod two reactions run concurrently, viz. :—

- (1) a primary light reaction, of which the light requirements are relatively high, and which leads to the formation of a substance 'A'.
- (2) a secondary light reaction with low light requirements, which leads to the formation of 'X' from a substrate 'S', produced by a slow non-photochemical reaction. This reaction is held to be that which is involved in low intensity supplementary illumination.

The formation of 'X' also occurs during a light-break, and the inhibiting effects observed in Carr's experiments with *P. ocymoides* and *X. pennsylvanicum* are held to be due to the addition of the 'X' formed during the 'light break' to that formed during the nearest main light period, so that the total quantity of 'X' is raised to a level which completely inhibits the formation of 'B' from 'A' (which can only occur during the initial hours of darkness, when a high level of 'A' is available).

The following modification of the scheme put forward by Gregory (1947) for short-day plants is suggested :—



Evidence was brought forward in support of the view that in long-day species flowering is promoted by 'X' and inhibited by 'B', i.e. the situation is the converse of that in short-day species.

REFERENCES.

- CARR, D. J. 1952. *Physiol. Plant.*, **5**, 70–84.
 GREGORY, F. G. 1947. *Symp. Soc. Exp. Biol.* (Cambr.), **2**, Growth.
 WAREING, P. F. 1950. *Physiol. Plant.*, **3**, 258–276.
 —. 1951. *Physiol. Plant.*, **4**, 41–56.

PHOTOPERIODISM IN THE CHRYSANTHEMUM AND ITS RELATION TO VERNALIZATION

By W. W. SCHWABE. Research Institute of Plant Physiology, Imperial College of Science and Technology, London.

Since most of the results of the investigations described in this communication have been published previously (*Journal of Experimental Botany*, Schwabe, 1950 etc.) they are only briefly summarized here.

In the flowering of the Chrysanthemum two stages can be distinguished fairly naturally. They are the initiation stage and the stage of further development of the potential inflorescence bud once it has been initiated.

Previously it was thought that the only environmental factor controlling flowering in the Chrysanthemum was the length of day, short day leading to flowering, long day preventing it. However, some experiments by Dr. Holdsworth in the years 1947 and 1948 showed that this was not the only factor concerned, and consequently the flowering behaviour of the Chrysanthemum has been subjected to a complete re-examination. The following results were obtained :—

Bud initiation was found to be largely dependent on a temporary exposure to low temperature—i.e. vernalization. Treatment for 3–4 weeks gave the maximum effect. This cold treatment may be interrupted daily by periods at normal greenhouse temperature. Cold treatment during the hours of darkness appeared more effective than during the day. There is no doubt that under ordinary horticultural practices this cold requirement is easily satisfied and would not normally be apparent. A striking effect noted was the diageotropic growth habit of unvernallized plants grown in short-day conditions. Basal shoots produced on plants whose main shoots have begun to die down after flowering need to be vernalized again. Attempts to de-vernalize plants by heating them to about 40°C immediately after the end of the vernalization treatment indicated that heat de-vernalization does not occur.

Inflorescence initiation is delayed by continuous long-day treatment, but limited periods of long day given before or very soon after the end of the vernalization treatment are found actually to hasten flowering. The effect of this treatment is maximal with full vernalization, but insignificant in unvernallized plants.

The further development of inflorescence buds has also been investigated. Potential inflorescence buds produced in long day do not normally produce open flowers. They are arrested almost as soon as they become macroscopically visible, and vegetative lateral shoots grow out from the uppermost leaf axils. When maintained in long days inflorescence development does not proceed beyond the formation of a bare receptacle: no florets are produced. These are the 'breakbuds' of the horticulturist. Their further development can be procured by (1) transfer to short day, (2) removal of all lateral shoots in long day, and (3) by rooting the detached inflorescence in long day.

Inflorescence buds produced in short days can be inhibited (1) by transfer to long days, (2) by reduction of the light intensity in short days, and (3) by application of auxin paste in short days. All three inhibitory treatments are effective only in the early stages of development of the bud. The latest stage at which an inflorescence bud was found to have been inhibited was that of ovule formation in the ovaries of the larger marginal florets.

A number of teratological effects noted in those plants induced to produce open flowers in spite of long-day treatment included the production of bracts—other than the outer involucre bracts—inserted between the florets. This

is of interest as the absence of bracts on the receptacle is regarded as one of the distinguishing characters of the subtribe of the Compositae of which *Chrysanthemum* is the type genus.

Finally it should be pointed out that in a plant with so many divergent varieties, there will clearly also be differences in response to environmental factors, but no indication has been found that these differences are other than merely quantitative.

LITERATURE CITED.

- SCHWABE, W. W. 1950. Factors controlling flowering in the *Chrysanthemum*.—I. The effects of photoperiod and temporary chilling. *J. Exp. Bot.*, **1**, 329–43.
 —. 1951. Factors controlling flowering in the *Chrysanthemum*.—II. Day-length effects on the further development of inflorescence buds and their experimental reversal and modification. *Ibid.*, **2**, 223–37.
 —. 1952. Factors controlling flowering in the *Chrysanthemum*.—III. Favourable effects of limited periods of long day on inflorescence initiation. *Ibid.*, **3**, 430–36.

PHOTOPERIODISM AND VERNALIZATION IN CEREAL PLANTS

By O. N. PURVIS.

Spring rye is a true long-day plant, flowering earliest in complete absence of darkness. Unvernalized winter rye is very slow to flower in any constant day-length, but is earliest in continuous light. A more effective light treatment for unvernallized winter rye is, however, a period under short days followed by long days or continuous light. (Short-day induction.) The optimal period in short days is about six weeks; longer treatment retards flowering.

Completely vernalized winter rye behaves as spring rye, and the effect of sub-optimal periods of vernalization is related to their duration in a way that indicates the vernalization reaction to be autocatalytic. Incomplete vernalization is partially reversible by high temperature, but as the process nears completion it becomes progressively more stable to heat. It is suggested that the process is a chain of reactions from a precursor 'A' to a substance 'B'. The first part of this chain is reversible and the last irreversible. In this way the increasing stability to heat may be explained. This substance 'B' is present in spring rye, and in winter rye it accumulates during vernalization. Without vernalization its concentration is very low, but during growth it accumulates slowly at the apex. The reactions from 'B' depend on its concentration and on the day-length, and determine how many leaves shall be produced before flower differentiation shall occur.

The fact that the flowering of winter rye can be accelerated by both short days and continuous light can be attributed to a change in its photoperiodic requirement with progressive development. The results of an experiment carried out by Dr. M. B. Gott at Imperial College confirm this. When plants were given a period in short days followed by continuous light, short-day induction was observed; as the short-day period increased up to six weeks, flowering was progressively accelerated, but further short-day exposure retarded flowering. When, however, continuous light preceded the short-day treatment, there was no effect with exposures up to six weeks; indeed, there was some indication of retardation. Longer exposure to continuous light accelerated flowering up to the maximal value obtained with continuous light throughout. Thus, winter rye behaves as a short-day plant for some six weeks after planting, but after this point is reached, it reacts as a long-day plant.

PHOTOPERIODIC RESPONSES OF ARABIDOPSIS THALIANA

By F. G. GREGORY and G. G. HUSSEY. Research Institute of Plant Physiology, Imperial College of Science and Technology.

Long-day plants are defined as those which flower with the least delay in continuous light. Two categories may be distinguished, those which may be termed 'obligate' remain vegetative indefinitely when exposed to daylengths that are shorter than a certain critical duration, as for example *Hyocymus niger* which will only flower under normal conditions when the photoperiod is in excess of 11 hours. Other long-day plants, notably the cereals, eventually initiate flowers even in short days; these may be termed 'facultative' types. With increasing duration of darkness in each 24-hour cycle the onset of the reproductive phase is retarded, but there is no definite critical day-length below which flowering is eliminated.

Arabidopsis thaliana (L.) Heynh., a small annual belonging to the Cruciferae, flowers most rapidly in continuous light; in short days flowering occurs but is considerably retarded. It may therefore be classed as a facultative long-day plant. Its value for photoperiodic studies was first noted by Laibach in 1943, who recommended its use on account of its small size and short life cycle.

Plants given 8 hours of daylight each day from 10 a.m. to 6 p.m. followed by 16 hours of darkness, remained vegetative for approximately 60 days when sown in early May 1951. Buds then became visible as the first macroscopic sign of flowering. When tungsten light of low intensity replaced the 16 hours of darkness, so that the plants received continuous illumination, the time to bud formation was progressively reduced as the intensity of the artificial light was increased up to 50 foot-candles. At this intensity buds were formed in about 25 days. Increasing the intensity of the tungsten light above 50 foot-candles had, however, little further effect on hastening bud formation.

Using tungsten light of 50 foot-candles it was possible to hasten progressively the time to budding by increasing the duration of the photoperiod by steps from 8 hours to 24 hours. Under a 12-hour photoperiod, that is when 4 hours of tungsten light followed directly the 8 hours' daylight given each day, buds were formed in 42 days; with 16 hours photoperiod, with 8 hours of tungsten light immediately following the 8 hours' daylight, buds appeared after 31 days. With supplementary tungsten light of 16 hours (continuous light or 24-hour photoperiod) buds were formed in 23 to 26 days.

The effect of various photoperiods on time to bud formation is shown in Table I, in which results for two experiments are given, each entry being the mean of 20 replicates.

TABLE I.

Length of light period 8 hr. daylight + supplementary tungsten light of 50 foot-candles	Days to flower bud formation	
	Expt. 1	Expt. 2
8 hrs.	59.9 ± 0.82	62.4 ± 1.1
12 hrs.	43.6 ± 0.89	42.2 ± 0.97
16 hrs.	30.8 ± 0.50	30.7 ± 0.66
24 hrs.	26.4 ± 0.47	25.4 ± 0.33

The previous experiments have dealt with effects of varying day-length on the time to budding when these treatments were given from the time of germination onwards.

Such experiments give no information on the changes of day-length requirement of the plant at various stages in growth. To investigate this point transfer experiments were undertaken, in which plants were removed from short day to continuous light and vice versa after varying number of days from germination. Short days here mean 8-hour exposures to normal daylight followed by 16 hours in darkness at constant temperature, and the continuous light regime consisted of 8 hours' daylight followed by 16 hours' tungsten light at 50 foot-candles also at the same constant temperature. The results of this experiment are presented in Table II.

TABLE II.

Short days given before C.L.	Total Days to Budding	No. of days in C.L.	Reduction in days C.L. brought about by preliminary S.D.'s
0	23.1	23.1	0
10	24.4	14.4	8.7
20	29.5	9.5	13.6
30	37.7	7.7	15.4
40	46.4	6.4	16.7
50	54.6	4.6	18.5
(58.5 short-day control)	58.5	0	23.1

Cycles of C.L. prior to S.D.'s	Total Days to Budding	No. of days in 'S.D.'s	Reduction in short-days brought about by preliminary C.L.
0	58.5	58.5	0
10	58.1	48.1	10.4
15	47.6	32.6	25.9
18	30.0	12.0	46.5
20	25.6	5.6	52.9
22	24.4	2.4	56.1
(23.1 C.L. control)	23.1	0	58.5

The first column in the table specifies the number of days from germination of the preliminary treatment, either short days or continuous light, before transfer to the alternative day-length. In column 2 are entered the total numbers of days to budding, and in column 3 the number of days required to establish flower buds after transfer from the preliminary treatment shown in column 1. In the last column is shown the *reduction* in time to bud formation consequent upon the preliminary treatment. By comparing the corresponding value in columns 1 and 4 the relative effects on bud formation of the two day-length regimes can be directly assessed. For example, 30 preliminary short days decrease the necessary number of days in continuous light by 15.4, whereas 15 preliminary cycles of continuous light reduce the number of short days required by 25.9.

The relative effects of continuous light and short days can be seen from the graph in fig. 1 in which the data in column 4 of the table are graphically presented. From this graph the effect of the preliminary treatment of a certain number of days of either regime can be directly assessed. By reading along the axis marked short days for the requisite number of preliminary days, the distance read off parallel to the other axis then gives the reduction in time required to form buds in continuous light; a similar procedure reading first along the vertical axis gives the reduction in time to flower in short days after a preliminary period in continuous light.

The circles represent the results of transfer from short days to continuous light, and the triangles transfer from continuous light to short days. It will be noted that all the points plotted fall upon a single curve, and the relative values of continuous light and short days on flower induction are shown by the slope of the curve at any point. It thus appears that for the first ten days from germination the effect of a day of continuous light is approximately the same as that of a short day, and that up to this stage the light requirement of the plant is independent of day-length. With increasing age of the plant one day of continuous light is progressively more effective than one short day up to approximately the half period of the vegetative cycle, but after this continuous light decreases in effectiveness.

The fact that all the points lie on a single curve indicates that irrespective of whether a particular point on the curve has been reached by a preliminary treatment of a certain number of cycles of either day-length the subsequent

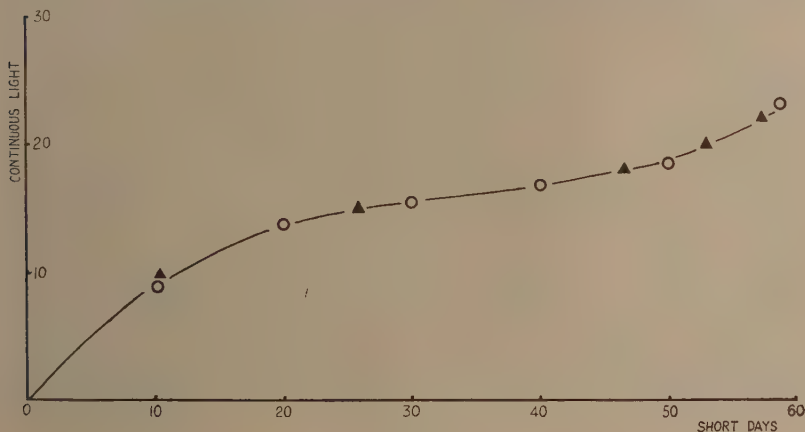


FIG. 1.

number of days required to reach flower bud formation in the two light regimes is unaffected. It may therefore be concluded that there are no after effects of the preliminary treatment, which would modify the subsequent light requirement and therefore the effects of long and short day treatments are independent.

Using this graph it is possible to make predictions of the number of days required to reach budding in either regime after exposing the plants to a given number of days in the alternative treatment at any time after germination; this has been verified experimentally with considerable accuracy.

DISCUSSION.

Dr. E. M. Delf commented on the interest and the extent of the field of work which had been presented. The ingenious interpretations put forward would no doubt need further testing. She asked whether there was any evidence as to how and by what path the unknown substances which promoted flowering travelled through the tissues from one region to another.

Prof. L. J. Audus asked of Dr. Wareing whether he was of the opinion that his substance 'X' might be identified with auxin and if so what this would imply to be the nature of its antagonist, substance 'B'.

**PROCEEDINGS OF THE GENERAL MEETING HELD
20 March 1952**

Colonel F. C. STERN, O.B.E., M.C., Vice-President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 6 March 1952, having been circulated, were taken as read, and confirmed.

The Vice-President in the Chair welcomed the Members of the Systematics Association at the Meeting.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. A. E. Blake, K.L.B., Prof. Dr. Jean Feldmann, F.M.L.S., Dr. S. M. Manton, F.R.S., Mrs. G. Montgomery, Mr. Richard Morse, The Hon. W. L. Palmer and Prof. F. E. Weiss, F.R.S.

The Vice-President in the Chair reported the death of Prof. Frederick Tom Brooks, C.B.E., F.R.S., and Thomas Bainbrige Fletcher, R.N., Fellows of the Society.

Certificates of recommendation for election to Fellowship were read for the first time, in favour of the following candidates :—John Patrick Micklethwait Brenan, M.A., Miss Kathryn Benson-Evans, M.Sc., Francis Jessop Bingley, M.A., A. J. Boerman, M.D., Dr. Margaret Elizabeth Brown, M.A., Prof. C. G. C. Chesters, Douglas Graham Cowden, B.Sc., John Heslop Harrison, M.Sc., Ph.D., Thomas Raeside Laycock, B.Sc., Aleksandrs Melderis, Ph.D., Mahmoud Ahmed Melouk, M.Sc., Ph.D., Francisco D'Ascensão Mendonça, Denys Morgan, B.Sc., S. K. Mukerjee, M.Sc., Ph.D., Mrs. Elsie H. Purnell, M.A., A. R. Ranjha, Prafulla Chandra Sharma, M.Sc., Kenneth Swinburne, Mrs. Sybil Alice Stern, Alasdair Ramsay Tainsch, M.B.E., B.A., Bernard Verdcourt, B.Sc., A.L.S., Owen Lynden Wade, M.A., M.D., M.R.C.P.(Lond.), A.L.S., and Derek Oliver Weitzel, B.Sc.

A Joint Discussion with the Systematics Association :—

‘Growth and Systematics’ was held, which was opened by Prof. W. E. Le Gros Clark, F.R.S., Dr. R. M. C. Eagar and Dr. R. Melville.

A general discussion followed, in which the following took part :—

Prof. J. B. S. Haldane, F.R.S., Dr. Sylvester Bradley and Dr. W. B. Turrill; Dr. R. M. C. Eagar and Prof. W. E. Le Gros Clark replied.

**GROWTH AND BODY PROPORTIONS IN RELATION TO THE
SYSTEMATICS OF THE HIGHER PRIMATES**

W. E. LE GROS CLARK.

Department of Anatomy, University of Oxford.

In discussions on the inter-relationships of the primates considerable emphasis has sometimes been laid on differences in body proportions. It has been argued, for instance, that the relatively long arms and short thumbs of the anthropoid apes indicate such a wide separation from the Hominidae as to preclude any close relationship at all. On the other hand, systematic metrical studies carried out during the past twenty years or so have

demonstrated (1) that these differences are not actually so marked as at first sight they appear to be and (2) that some of them only appear ontogenetically during late foetal or post-natal growth (Schultz, 1950). For example, the great average length of the lower limbs in man, relative to the trunk height, is a distinction from the anthropoid apes which does not appear till after birth, and, in fact, in individual adult gibbons and chimpanzees the relative length of the lower limbs may be actually greater than in some human beings even when growth is completed. The shortness of the upper limb relative to the lower limb is quite a distinctive feature of modern man, the intermembral index being well below 100 in the adult. But in early foetal life it is over 130, and at this stage is therefore equivalent to indices commonly found in catarrhine primates. The arms of the gibbon only reach their maximum relative length after birth. The modern human thumb appears relatively longer than in the anthropoid apes only because the fingers have not extended their length as they have done in the latter. The great length of the big toe which appears to be so characteristic of *Homo* is simply a relative phenomenon due to the great shortening of the lateral toes. These studies of variations in the relative growth rates of the trunk and limbs have served to emphasize that the differences between the main groups of higher primates may not be so fundamental as some had supposed, and it is no doubt partly due to this that there is now a tendency to approximate the Pongidae (anthropoid ape family) and the Hominidae rather more closely in taxonomic systems. In Simpson's classification these two families are grouped together in the superfamily Hominoidea and are thus contrasted with the catarrhine monkeys, Cercopithecoidea.

If differences in linear proportions were the main distinguishing features of the trunk and limbs of the Hominidae and Pongidae, there would be little theoretical difficulty in postulating the derivation of one from the other in evolutionary development. But they are, of course, related to structural modifications associated with very different modes of life, and it remains true to say that, after their phylogenetic divergence from a presumed common ancestry, the Pongidae and Hominidae must have followed very different developmental trends. The former became progressively adapted for an arboreal existence which involved the development of limbs for a specialized type of brachiation. The latter became progressively adapted for an erect bipedalism on the ground. There is good reason to suppose that these divergent trends in posture and gait must have been initially responsible for the separation of the hominid from the pongid sequence of evolution, i.e. before other distinguishing characters such as those shown in the absolute size of the brain and the relative size of the jaws manifested themselves. Thus, a study of the fossil remains of early hominids in the Far East, *Pithecanthropus*, indicates that, in spite of the small size and primitive proportions of their brain and the massive character of their jaws and teeth, they were equipped with limbs which (so far as the rather fragmentary evidence goes) appear already to have been indistinguishable from those of *Homo sapiens*. The discovery of the Australopithecinae in South Africa, again, has demonstrated a rather similar combination of characters, i.e. the association of remarkably ape-like dimensions of brain-case and jaws with details of skull structure, dentition and limb skeleton which (it is now generally agreed) are hominid rather than pongid (Broom *et al.*, 1950; Le Gros Clark, 1950, 1952). In particular, the conformation of the pelvis (known from three specimens of the *os innominatum* discovered at different sites independently) makes it reasonably certain that they were capable of an erect posture and gait closely approaching that characteristic of *Homo sapiens*. All this direct palaeontological evidence, combined with the less direct (but also important) evidence of comparative anatomy, leads to the inference that the really significant factors which

determined the segregation of the Hominidae as a separate family of the Hominoidea were the differential adaptations of the locomotor apparatus (Washburn, 1950). If this is accepted, it follows that, in assessing the taxonomic position of small-brained fossil hominoids whose status may be otherwise uncertain, evidence of structural adaptations to posture and gait may be of primary importance.

It seems to have been assumed by many authorities that fossil anthropoid apes of Pliocene, Miocene and Oligocene times—creatures which have been identified as early representatives of the Pongidae on the basis of the morphological details of their jaws and teeth—were similar to the Recent anthropoid apes in the construction of their limbs. And since the limb proportions of the Recent apes show certain specializations in their differential growth rates which have been avoided in the Hominidae, it has also been assumed (1) that the latter could not have been derived from the Pongidae and (2) that their evolutionary independence must therefore have a vast antiquity. But there was never any valid reason to suppose that these early representatives of the Pongidae had already developed the specializations characteristic of their later representatives. On the contrary, it might have been expected (on the analogy of other palaeontological sequences in mammalian evolution) that in the early stages of pongid evolution the limbs would still have preserved many primitive characters such as those which are still retained in the Recent catarrhine monkeys. It is now known that this was the case (Le Gros Clark & Leakey, 1951; Le Gros Clark & Thomas, 1951).

One of the most important discoveries made by the British-Kenya Miocene Expedition in recent years is that of portions of the limb skeleton of Early Miocene apes. These demonstrate quite clearly that the limbs were not specialized, as in the Recent apes, for brachiating habits. They show numerous resemblances in their proportions and morphological details to the limbs of cercopithecoid monkeys, and indicate a similar type of quadrupedal gait (whether along the branches of the trees or on the ground). These conclusions fit in very well with other discoveries made in Europe. As long ago as 1887 Depéret described a metacarpal bone found in association with a mandibular fragment of *Pliopithecus*, but he was puzzled by the fact that, although this fossil ape is generally accepted as an early type of gibbon (on the basis of dental morphology), the metacarpal bone resembled rather that of a cercopithecoid monkey (Depéret, 1887). Quite recently, the skeletons of three specimens of *Pliopithecus* have been found at Neudorf in Austria. At the time of writing only a short preliminary note on this important discovery has appeared (Zapfe, 1952), and it is clear from this that the limbs of these Middle Miocene apes also preserved primitive proportions associated with a quadrupedal gait, and showed none of the specialized characters of the modern apes. Thus, so far as the proportions and structural adaptations of the limbs are concerned, there now appears to be no theoretical objection to the derivation of the Pongidae and the Hominidae from a common ancestry at least as late as Early or Middle Miocene times. It was subsequent to this time, therefore, that, in association with opposing trends in adaptation to posture and gait, the divergent evolutionary development of characteristic differential growth rates of the limbs and trunk in the Hominoidea must have marked the initial phylogenetic separation of the earliest precursors of the Hominidae from the Pongidae. As already noted, the manifestation of these divergent trends would clearly provide one of the most reliable indications of the taxonomic distinction between the early hominids and the precursors of the modern anthropoid apes. Unfortunately, however, with the single exception of the Eppelsheim femur (? *Dryopithecus*) nothing is known of the limb skeleton of fossil hominoids during the early Pliocene or late Miocene periods. The Australopithecinae are probably referable either to the end of the Pliocene

period or the beginning of the Pleistocene, and in this case the evident modification of the limbs (and certain features of the cranial base) for erect progression, as well as numerous morphological features of the skull and dentition (Bronowski & Long, 1952; Broom *et al.*, 1950; Le Gros Clark, 1950) has now led a number of authorities to the view that they are more logically grouped with the Hominidae than the Pongidae. Indeed, one systematist of considerable experience has suggested that the anatomical resemblances between the South African fossils and *Homo* are sufficiently striking to warrant their inclusion in the same genus (Mayr, 1950). It would be out of place here to consider in detail the taxonomy of the South African fossils. Their allocation to several different genera will not be acceptable to most systematists; indeed, on purely morphological grounds even specific distinctions have yet to be justified*. Until agreement has been reached on these vexed questions, therefore, it is convenient to refer to each local population by the place name of the site of their discovery, and to the whole series as the Australopithecinae (even though, as I think very probable, it will eventually be agreed that their distinction from *Homo* is at the most a generic one). As I have previously emphasized, in spite of the intermediate appearance presented by their total morphological pattern it does not necessarily follow, of course, that the South African representatives of the Australopithecinae were themselves ancestral to *Homo sapiens*. On the other hand, the morphological evidence makes it probable that *some* representatives of this zoological group—perhaps elsewhere and at an earlier date—may have been so.

One of the remarkable features of the Lower Miocene apes from East Africa is the great diversity in their body size which, at least so far as the dentition is concerned, does not appear to be correlated with any marked divergence in morphological particulars. Thus, three species of *Proconsul* have been identified mainly on the basis of size, but because of individual and (?) sexual variation in each group it was difficult at first to separate them with certainty. With the accumulation of additional material, however, it has been possible to obtain more reliable information on their range of variation, and the distinctions between them have become more obvious and assured. Nevertheless, they do form a very closely graded series, and it remains an interesting observation that the marked contrasts in body size are accompanied by relatively slight differences in morphological detail. The smallest species of *Proconsul* (*P. africanus*) is about the size of a pygmy chimpanzee (*Pan paniscus*), and the largest species (*P. major*) reaches the dimensions of a large gorilla. The evidence of these East African Miocene apes (and also that of Miocene and Pliocene apes from elsewhere) suggests rather strongly that in the evolution of the Hominoidea diversification in size occurred relatively early and preceded diversification in structural details. There is some evidence, also, that a similar process occurred in other early groups of primates, e.g. *Adapis* (cf. *A. sciureus*, *A. parisiensis* and *A. magnus*). This is a phenomenon which appears not to be characteristic of mammalian evolution generally, for while there is a common tendency for natural selection to favour a body size slightly above the mean, so far as I am aware early diversification in size without diversification in morphological details is at least unusual. Possibly the phenomenon is related to the arboreal mode of life typical of the primates, for it seems reasonable to suppose that differences in size must quickly lead to a sort of ecological stratification among the branches. And this, again, as an isolating mechanism would favour rather rapid speciation.

* In a recent review (Zuckerman, 1950) it is stated that I regard all the South African fossil 'apes' as generically distinct from one another. In fact, I have not held this opinion.

For example, the smallest forms, by confining their activities mainly to the more attenuated branches of the tree tops would lead a secluded life within the protection of foliage and thus be ecologically segregated from larger forms. Because of the nature of their immediate environment, many of them would probably tend to develop nocturnal and insectivorous habits. The medium-sized forms would find their natural environment mainly among the larger boughs and, by developing their capacity for running and leaping along the latter, would be able to extend their range very considerably by rapidly moving from tree to tree across wide stretches of jungle. They would seek protection from enemies not so much by obscuring themselves as by their speed and agility and by a tendency to form cooperative groups. The largest forms, e.g. *Proconsul major*, must presumably have been restricted by their size and weight to the main branches of the trees at lower levels near the ground; moreover, they would be capable of contending with possible enemies on the ground which might prevent smaller species from leaving the shelter of the trees. Excursions on the ground would extend their natural habitat to allow for a much greater range of food-gathering (like the modern gorilla) and would also confer an additional advantage which, in view of the following considerations, had perhaps a special significance in East Africa during the Early Miocene. It seems probable that the evolution of ground-living forms in the ancestry of the Hominidae may have been the result of adaptations primarily concerned, not with the abandonment of arboreal life, but (paradoxically) with an attempt to *retain* it. For in regions undergoing gradual deforestation they would make it possible to cross intervening grasslands in order to pass from one forested area to another*. A preliminary study of fossilized fruits and seeds (as well as the evidence of the faunal assemblage) indicates that the general environment of *Proconsul* was just of this type, consisting of wooded valleys of limited extent separated by open savanna country. The evolution of such large apes as *P. major* in the Lower Miocene of East Africa, therefore, is clearly of considerable interest, for the reason that their size (combined with the nature of the local terrain) would certainly provide the opportunity and incentive for some degree of terrestrial activity. The structural adaptations induced by this activity in apes whose limbs (unlike those of the gorilla) still preserved the primitive catarrhine proportions might provide evidence of particular significance for the problem of the early adaptations of ground-living hominoids. Unfortunately, except for fragments of the clavicle no limb bones of this particular species (*P. major*) have yet been found.

The recent accessions of so many fossil remains of early primates have made it possible to define certain evolutionary trends in structural modification, and thus to provide more certain criteria for determining the taxonomic status of extinct forms. In particular it is possible to distinguish with much more assurance between 'specialized' and 'primitive' characters. For example, it has long been maintained by some anatomists that the strong, conical and pointed canines and the sectorial premolars of anthropoid apes are specialized features, compared with the brachyodont, spatulate canines and bicuspid premolars of *Homo* which have been assumed to be more 'primitive' or 'generalized'. On the basis of this distinction, it has been argued that the whole group of anthropoid apes represents a very specialized divergent line of primate evolution and that the Hominidae could not therefore have been derived from an anthropoid ape ancestry. Many types of fossil Pongidae are

* This proposition is parallel to the interesting conjecture that water-living vertebrates initially acquired terrestrial and air-breathing adaptations in order to preserve their aquatic mode of life. The suggestion is that, in times of drought, these adaptations made it possible to escape from dried-up rivers or pools and to go over-land in search of water elsewhere.

now known from Miocene and Pliocene levels in Europe, Asia and Africa, and in all of them, without exception, the canines and premolars show the same fundamental characters as those of Recent apes. In other words, the palaeontological evidence is strongly against the suggestion that these are specialized features of relatively late development. It has become more probable, indeed, that the hominid characters of the canine and premolar teeth have arisen as modifications of teeth of a pongid type, and that these modifications occurred probably in the late Miocene or the Early Pliocene. Other examples might be given to illustrate the misconceptions which have arisen from too confident statements of comparative anatomists on what is to be regarded as 'primitive' and what 'specialized'—misconceptions which have not infrequently led to a distorted and (it seems) inverted interpretation of hominid phylogeny. It is certainly true to say that the accumulation of palaeontological evidence has added strong emphasis to the more usual interpretation of the comparative anatomical evidence—that the Hominidae and the Pongidae are phylogenetically quite closely related, and that the divergence of these two families probably occurred not earlier than the Miocene period.

A problem of some difficulty and importance concerns the precise taxonomic status of the extinct apes of Miocene time. Commonly they are included in the anthropoid ape family, the Pongidae. It has been argued, however, that since this term was originally defined by reference to the modern anthropoid apes which are characterized by certain specializations in limb proportions, etc., it can hardly apply to extinct genera in which (as is now known) these specializations were not fully developed. One anatomist, indeed, has complained that in their combination of cercopithecoid and hominoid features the Miocene apes seem to occupy a kind of taxonomic purgatory (Straus, 1949). In a sense, of course, this is perfectly true, but it has to be recognized that in the course of their evolution every zoological group must presumably at some time pass through a taxonomic purgatory. In the case of the Miocene apes, their inclusion in the Pongidae appears valid for the following reasons:—(1) a taxonomic category should naturally include not only the terminal products of its evolution, but also the earlier phases of development through which it passed after it became definitely segregated from immediately related groups; (2) it is to be expected that the earlier representatives of the Hominoidea, after their initial segregation from the Cercopithecoidea, would retain primitive characters of a cercopithecoid type which became lost in the course of later evolution; (3) there is good evidence that the Cercopithecoidea had in fact already become a separate and well-defined group by the Early Miocene, for fossil remains of a cercopithecoid monkey, provisionally identified as *Mesopithecus* (MacInnes, 1943), have been recovered from the Miocene deposits of East Africa showing the specialized dental features distinctive of the whole group; (4) the dental morphology of the Miocene apes approximates very closely to that of the Recent Pongidae, and in certain elements of the dentition (e.g. the canines and premolars) appears to be indistinguishable; (5) a difference in limb proportions does not by itself provide an adequate basis for a family distinction; (6) in spite of their general cercopithecoid appearance, the limb bones of some of the Early Miocene apes (e.g. *Limnopithecus*) do show certain features in which they approximate to Recent Pongidae. If all these factors are given due consideration, it seems reasonable to include these extinct genera of fossil apes (so far as they are at present known) in the Pongidae, though it may be justifiable to accord them a sub-familial distinction.

In the evolution and taxonomy of the Hominoidea the differential growth of the brain comes to assume an outstanding significance. Yet it is important to recognize that the large brain of *Homo sapiens* may not be taken as a

criterion of the Hominidae as a whole. This becomes evident enough if attention is given to the following considerations. There is general agreement that the divergence of the Hominidae from the Pongidae probably dates back to the Miocene period (or possibly earlier), and almost certainly not later than the early part of the Pliocene. In other words, the segregation of the Hominidae as a distinct zoological group occurred hardly less than ten million years ago. On the other hand, the palaeontological evidence seems to make it clear that the expansion of the brain from simian dimensions did not become obtrusive till the beginning of the Pleistocene or perhaps the end of the Pliocene, that is to say, about one million years ago. It follows, therefore, that for a matter of at least several million years the earlier representatives of the hominid line (or lines) continued to retain a brain size which would not by itself have distinguished them from the Pongidae. That this fact is not always fully appreciated has been made particularly clear in recent discussions on the taxonomic status of the Australopithecinae. It also needs to be recognized that the continued retention of a small brain during the earlier phases of hominid evolution would necessarily be associated with the retention of those primitive characters of the skull which are secondarily related to it (and which only disappear in later phases as the result of the growth of an expanding brain case). An obvious example of this is the low sagittal crest found to be present in two of the australopithecine skulls found at Swartkrans. Because of its association with definitely hominid traits in the dentition and skeleton, this seems to have caused some surprise. But a median sagittal crest is not a morphological entity having a separate genetic basis; it is the secondary result of a growth process depending on the combination of a small brain-case with large jaws and temporal muscles, and it is for this reason that it is found in all genera of the Pongidae. It is normally strongly developed in mature male gorillas and quite commonly in orangs. It may also be sometimes found in chimpanzees, and very occasionally in gibbons. Regarded in this light, it would be a matter for some surprise if the earlier small-brained representatives of the Hominidae did not also show a tendency for the development of a sagittal crest, for only as a result of the later expansion of the brain (and the concomitant reduction of the jaws) would the temporal muscles during growth always find adequate accommodation on the brain-case itself. In some respects, it is interesting to note, the sagittal crest of the australopithecine skull is very different from that of the modern large apes. In the latter it is always associated with a high nuchal crest. In the Australopithecinae, on the other hand, it appears to have been much more comparable with the low sagittal crest which may occasionally be found in the Siamang gibbon and which (according to Schultz) is limited to the posterior half of the frontal arc and the anterior half of the parietal arc.

The sequence of dental eruption is a growth process which has particular significance in the taxonomy of the primates. The important comparative studies of Schultz (1950) have shown that in the most primitive primates none of the deciduous teeth is shed or replaced before the eruption of all the permanent molars. In other words, the growth period of the animal as a whole is sufficiently brief for the deciduous teeth to continue functioning throughout without the disadvantage of excessive wear. In the ascending scale of primates there is a progressive acceleration in the replacement of the milk dentition relatively to the eruption of the permanent molars, and in most monkeys and all genera of anthropoid apes the incisor teeth erupt before the second permanent molar, and the two premolars before the last molar. But the canine teeth are still very late in their replacement, not completing their eruption until well after that of the second molar. This order of dental eruption is retained in certain fossil hominids (e.g. *Pithecanthropus*), and even in some groups of *Homo sapiens* a similar pattern is found. But in most modern races the replacement of the deciduous teeth takes still further precedence

over the eruption of the permanent molars. The first incisor tooth may occasionally erupt before the first permanent molar, and all the deciduous teeth (including the canines) are replaced before the eruption of the second and third molars. Schultz has suggested that this tendency for a relative acceleration in the replacement of the deciduous dentition in *Homo sapiens* is simply related to the fact that, the period of growth being greatly prolonged, the teeth (which are no more durable than those of other primates) need to be replaced at a relatively earlier date. The prolongation of the growth period is a significant development in which the Hominidae as a whole have come to be contrasted rather strongly with the lower primates. It is therefore of unusual interest that, as reported by Broom & Robinson (Broom *et al.*, 1950), the abundant remains of the fossil Australopithecinae found at Swartkrans provide evidence of a sequence of tooth eruption corresponding, not to the pongid pattern, but to that characteristic of *Homo*. In particular the permanent canine tooth (in conformity with its reduced size) erupted relatively early. Clearly, this feature has an important relevance to the question of the taxonomic position of the Australopithecinae. Although remains found elsewhere (at Makapansgat) show that in some representatives of this fossil group the eruption of the canines occurred later, this does not affect the taxonomic importance of the sequence of eruption found in the Swartkrans fossils, for, as already noted, a late eruption of the canine is also characteristic of *Pithecanthropus*, and certain types of modern man. On the other hand, the pattern of dental replacement characteristic of *Homo sapiens*, and also present in some of the Australopithecinae, has never been found to occur in any of the Pongidae, Recent or extinct.

In recent discussions on the taxonomic position of fossil hominoids, there is one source of confusion to which attention should particularly be drawn—the too frequent use of the colloquial terms ‘man’ and ‘human’. The fact is that these terms may not properly be used as equivalent to the zoological term ‘Hominidae’ and its adjectival form ‘hominid’ in the same way that (for example) the term ‘horse’ can be substituted for ‘equid’. In the latter case, although the primitive equid *Hyacotherium* is so very different superficially from the modern *Equus*, it can be called a primitive horse without real danger of misunderstanding, for the term ‘horse’ still remains elastic enough in the minds of most people to permit its extension to ancestral forms. Similarly, the fossil Hominoidea of Miocene age may appropriately be called primitive ‘anthropoid apes’, even though they had not acquired all the specialized features which are accepted as characteristic of the anthropoid apes of to-day. But the terms ‘man’ and ‘human’ have come to assume, in common usage, a much narrower and more rigid connotation which for most of us, however we may try to persuade ourselves otherwise, also contains a very real emotional element. There can be little doubt that if these colloquial terms were to be rigidly excluded in discussions on the evolutionary origin of *Homo*, and only the scientific terms proper to taxonomy employed, such problems could be approached on a much more objective plane than often appears to be the case*.

* The confusion to which the loose use of the term ‘man’ may give rise is well illustrated by those comparative studies, sometimes based on statistical analysis, in which the skeletal elements of a fossil hominoid are compared with only the Recent anthropoid apes and with only *Homo sapiens* (or perhaps even with only one or two racial varieties of *Homo sapiens*) and the conclusion is then drawn that in certain features the fossil agrees more closely with the ‘anthropoid apes’ than with ‘man’. The fallacy of such a statement is obvious, but it may nevertheless be very misleading to the casual reader. Clearly the authors of such studies are using the term ‘man’ as though it were equivalent to *Homo sapiens*, or perhaps only one racial variety of *Homo sapiens*. But the term ‘man’ must be taken also to include extinct types such as Neanderthal man and the various representatives of the *Pithecanthropus* group (including ‘*Meganthropus*’). These should be taken into consideration, and also, of course, all the known *extinct* types of anthropoid ape. The fallacy of extrapolating from single species or genera to larger taxonomic groups is not uncommon in the literature of palaeoanthropology.

If we accept the definition of 'man' or 'human' as indicating a tool-making creature (as reasonably advocated by Oakley, 1951), then the earlier small-brained representatives of the Hominidae which had not yet developed this capacity may be most conveniently referred to "the prehuman phase of hominid evolution".

REFERENCES.

- BRONOWSKI, J. & LONG, W. M. 1952. Statistical Methods in Anthropology. *Nature, Lond.*, **168**, 794.
- BROOM, R. & ROBINSON, J. T. 1951. Eruption of the Permanent Teeth in the South African Fossil Ape-men. *Nature, Lond.*, **167**, 443.
- BROOM, R., ROBINSON, J. T. & SCHEPERS, G. W. H. 1950. The Sterkfontein Ape-Man, *Plesianthropus*. *Transv. Mus. Mem.*, **4**.
- DEPÉRET, C. 1887. Études paléontologiques dans le Bassin du Rhône. *Arch. Mus. Hist. nat. Lyon*, **4**, 45.
- LE GROS CLARK, W. E. 1950. New Palaeontological Evidence bearing on the Evolution of the Hominoidea. *Quart. J. geol. Soc. Lond.*, **105**, 225.
- . 1952. Hominid Characters of the Australopithecine Dentition. *J. R. anthrop. Inst.*, **80**, 37.
- LE GROS CLARK, W. E. & LEAKEY, L. S. B. 1951. The Miocene Hominoidea of East Africa. *Fossil Mammals of Africa*, No. 1. British Museum (Nat. Hist.).
- LE GROS CLARK, W. E. & THOMAS, D. P. 1951. Associated Jaws and Limb Bones of *Limnopithecus macinnesi*. *Fossil Mammals of Africa* No. 3. British Museum (Nat. Hist.).
- MACINNES, D. G. 1943. Notes on the East African Miocene Primates. *J. E. Afr. Ug. nat. Hist. Soc.*, **17**, 141.
- MAYR, E. 1950. Taxonomic Categories in Fossil Hominids. *Cold Spr. Harb. Symp. quant. Biol.*, **15**, 109.
- OAKLEY, K. P. 1951. A Definition of Man. *Sci. News*, **20**, 69.
- SCHULTZ, A. H. 1933. Observations on the Growth, Classification and Evolutionary Specialization of Gibbons and Siamangs. *Hum. Biol.*, **5**, 212.
- . 1950. The Specialization of Man and his Place among the Catarrhine Primates. *Cold Spr. Harb. Symp. quant. Biol.*, **15**, 37.
- . 1950. The Physical Distinctions of Man. *Proc. Amer. phil. Soc.*, **94**, 428.
- STRAUS, W. L. 1949. The Riddle of Man's Ancestry. *Quart. Rev. Biol.*, **24**, 200.
- WASHBURN, S. L. 1950. The Analysis of Primate Evolution with particular reference to the Origin of Man. *Cold Spr. Harb. Symp. quant. Biol.*, **15**, 67.
- ZAPFE, H. 1952. Die *Pliopithecus*-Funde aus der Spaltenfüllung von Neudorf an der March. *Sonderab. a. d. Verh. geol. Bundesanst.*, **1**.
- ZUCKERMAN, S. 1950. Taxonomy and Human Evolution. *Biol. Rev.*, **25**, 435.

RELATIVE GROWTH IN SHELLS OF THE FOSSIL FAMILY ANTHRACOSIIDAE IN UPPER CARBONIFEROUS TIMES

By R. M. C. EAGAR.

(With 13 text-figures.)

INTRODUCTION.

In a paper read in an earlier Joint Discussion with the Systematics Association, Leitch (1951) reviewed some problems of systematics peculiar to the palaeontologist and discussed some of the methods by which the non-marine lamellibranchs of the Carboniferous Period have been studied and systematized during the past twenty-five years. In the following pages I have attempted to supplement Professor Leitch's paper by reviewing briefly, and mainly from the point of view of relative growth, the results of some recent studies on non-marine shells from the uppermost Millstone Grit and Lower Coal Measures of Yorkshire and Lancashire (fig. 1). Non-marine lamellibranchs are particularly numerous and well preserved in these measures and show a remarkable range of variation, both in internal features of the shell, as far as they may be examined, and in external features, notably in

their lateral outline (fig. 2). This paper also describes some attempts to investigate the latter type of variation, which has called for new or specially adapted methods of study and has raised several problems of systematics.

MEASUREMENT OF SHELLS AND CORRECTIONS FOR MODE OF PRESERVATION.

Measurements of shell length (L), height (H), length of anterior end (A) and thickness or obesity (T) have been measured in the standard manner, as defined by Davies & Trueman (1927), and illustrated in fig. 4*a, b*. Difficulties in taking these measurements tend to occur only when the line of the hinge is relatively short or the posterior dorsal margin strongly arched with oblique growth, as is sometimes the case in the genus *Anthracosia* (see Discussion in Eagar, 1952 d, pp. 371 and 373; and Trueman & Weir, 1951, p. 103).

Shells may also be measured in other ways (fig. 4*c*) when preservation is good. In fig. 4*c* the distance UG , the line of maximum shell growth from the umbo, has recently been measured by Deleers & Pastiels (1947) in a very detailed biometrical study of *Anthraconauta*. With the help of a camera, or

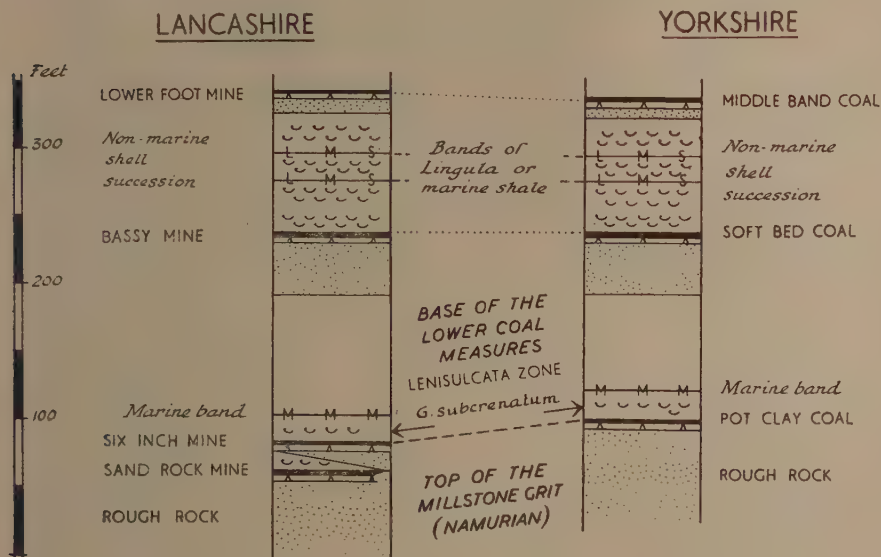


FIG. 1.—Sections to show the stratigraphical position of the non-marine shell bands, the faunas of which are mentioned in this paper. The arrow shows the position of the main band above the Six Inch Mine and Pot Clay Coal.

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camera lucida, the measurement of this dimension may well prove useful in future work on fossil shells, especially on those with oblique growth where there is a trend towards subtriangular outline. In this paper, however, results of statistical work on the Anthracosiidae are confined to those in which treatment has been given to dimensions measured in the standard directions.

As far as possible only uncrushed shells, or impressions from their external moulds, have been measured. In the case of small shells (under 28 mm. long) thickness of shell over the umbo may constitute as much as 8 per cent of the height of the internal mould (Eagar, 1947, p. 10 and fig. 6). Where it has been necessary to measure small internal moulds appropriate corrections have therefore been applied to convert their measurements to those of shells.

Lateral crushing, often to the extent of total flattening of the valves, is common amongst the larger shells and is also found amongst the smaller ones in fine-grained, well-laminated shales. Although in these cases the distortion of the lateral outline tends to be confined mainly to the umbonal region and to the anterior umbonal slope, lateral flattening undoubtedly tends to increase slightly the H/L ratio of a shell, especially when it is relatively long (H/L ratio less than 45 per cent), small and tumid. Since the comparison of crushed with uncrushed material is sometimes necessary (see p. 161) appropriate allowances can be made for this factor. For instance, from studies in shell communities where both modes of preservation may be found together (e.g. Eagar, 1947, p. 45, Table 7), it appears that total flattening may increase a mean H/L ratio of 42 per cent to as much as 45 per cent.

Crushing in any direction other than at right angles to the median plane of the valves seriously affects shell measurements. No measurements have therefore been taken on any shells in which there has been reason to suspect such crushing to have taken place.

THE VARIATION DIAGRAM OR PICTOGRAPH.

(a) General Principles.

Since the original development of the variation diagram or pictograph to illustrate assemblages or communities of fossils and to demonstrate continuous variation in several features taken together (Leitch, 1936, 1940, 1942), other workers have adapted the pictograph to suit the particular requirements of the material they have been investigating. When variation is comparatively small and can be largely defined in terms of shell measurements in a few different directions, the pictograph can be built in such a manner that its pattern merely reflects a plot of the measurements of the specimens, as was demonstrated by Aitken & McKerrow (1948) in a study of *Rhychonella boueti* Davidson. A simplified application of this principle may be seen in fig. 2 if only the central norm and the north and south series, which together form a continuous straight line, are considered. Northward from the norm the H/L ratio of the forms increases and southward it decreases, in both cases progressively, but the outlines of the shells in other respects preserve the essential form exhibited by the norm. Thus the whole series lies along a line in which the value of L remains approximately constant*, while that of H increases, more or less evenly, from south to north; and apart from a slight northward increase in the value of A , the length of the anterior end, there appears to be no further variable involved.

Dimensional 'control' of the positions of shells in fig. 2 does not, however, extend much further than this, since variation of the shell outline has proved too subtle for measurement (but see p. 155). There is, however, a more or less obvious dimensional basis for the general plan of arrangement of the radial series:

1. In the northern semicircle of the diagram (fig. 2) shells, when traced radially away from the norm, tend to show progressive increase in the H/L ratio, whereas in the southern semicircle the H/L ratio tends to decrease radially.
2. To the west of the norm the ventral margin of the shell straightens and finally becomes reflected, whereas to the east of it this margin becomes progressively more curved, so that the shell finally loses posterior inferior angulation.

* Differences in the size of shells shown in fig. 2 are briefly discussed on p. 153.

3. In the north-east and south-west directions shells show progressive expansion of the posterior end in slightly different ways, but in all cases develop the lateral outline characteristic of the genus *Anthraconaia*.
4. In the N.N.W. and S.S.E. directions the dorsal margin of the shell becomes arched, while the ventral margin becomes straight or slightly reflected.

A number of other series may be traced both within and between the main ones, both radially and to some extent in a circular manner around the norm. In fact transitions in both directions are more nearly complete than the diagram

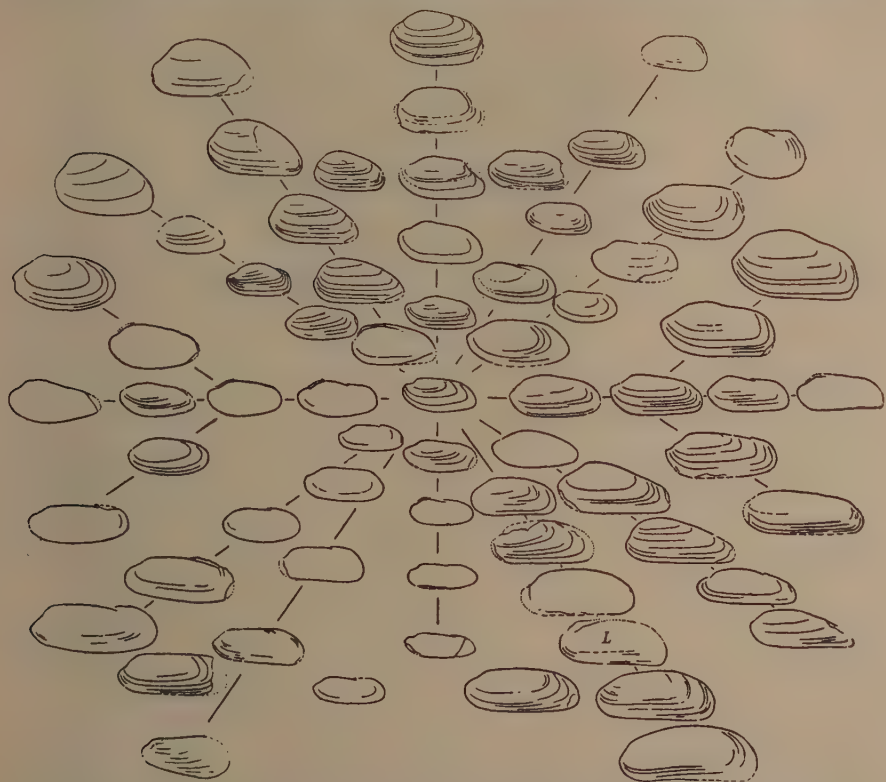


FIG. 2.—Part of the Standard Diagram (a variation diagram or pictograph) to show continuous variation around the norm of *Carbonicola fallax* Wright. All shells from above the Soft Bed—Bassy Mine, at half natural size.

[Reproduced, with slight modification, by permission of the Royal Society of London.]

suggests, since in the figure it was necessary to omit several forms, especially those lying between series, in order to keep the diagram clear and its size within reasonable limits.

(b) *Principles and Method of Construction of the Standard Diagram.*

The diagram shown in fig.2 was built up by the tedious adjustment of moveable tracings on a board which finally received more than 160 outlines of shells from various horizons between the Soft Bed and Middle Band Coal

of Yorkshire and the Lancashire equivalents of these seams, the Bassy and Lower Foot Mines (fig. 1). In these measures (fig. 10) it was necessary to examine the variation of successive, slightly different communities of shells, within each of which variation was usually continuous and often wide in range (fig. 11). Since it was found that every fauna had a few specimens very near the norms of the standard diagram (figs. 2, 3)*, it proved possible to



FIG. 3.—Part of the Standard Diagram, to show continuous variation around the norm of *Carbonicola protea* Wright (P). Numerous transitional forms have had to be omitted for lack of space. D. *Carbonicola discus* Eagar. H. *C. haberghamensis* Wright. All shells from above the Soft Bed-Bassy Mine, at half natural size.

[By permission of the Royal Society of London.]

build pictographs for each on the same general plan. Shells of similar trend were placed in the same directions with respect to a succession of very similar norms, the distance of each shell from the norm being controlled by reference to its position on the standard diagram; blanks were left when trends were unrepresented at any level. In other words a series of pictographs, illustrating

* Two distinct groups of shells were found, the first of *Carbonicola fallax* Wright, the norm of fig. 2, and the second of *C. protea* Wright, the norm of fig. 3, comprising a larger group of shells. The groups were evidently distinct before the deposition of the Soft Bed-Bassy Mine fossiliferous measures (p. 157).

successive, continuously variable communities, were superimposed on a pre-determined directional skeleton of variational trends which was kept constant. The method allows the easy comparison of slightly different faunas as was used for both the small and large shell groups (figs. 2 and 3 respectively) present in these measures (see fig. 11).

(c) *Growth Series and the Pictograph.*

In any assemblage of shells growth may be traced both by measuring the specimens over some range of size, and by a study of the larger individuals on which growth lines are clear and measurable. Fossil material usually exhibits an appreciable range in the size of the sample. Where variation is comparatively limited a considerable part of this range may be included in the pictograph without obscuring the general pattern reflecting the correlation of certain shape characters. In this way the pictograph does double duty in revealing also trends in relative growth. Thus in fig. 5 it will be apparent that the whole fauna tended to show considerable increase in H/L ratio with growth, but that this was somewhat less in Series 2 (figs. 5a, f, g, h, i) than in the remainder.

Where variation is very great, as in fig. 2, it is obviously necessary to keep size differences to a minimum. Differences in relative rates of growth of the shell in different directions are then revealed principally by growth lines, especially by those of the larger individuals. For instance, it will be apparent that the growth lines of several shells lying towards the periphery of fig. 2 reveal changes in shape during growth which are approximately those seen in the series linking these individuals to the more central forms, including the norm (see especially series passing outward to the N.N.W., N.N.E., E.N.E. and S.S.E.). In these series, as one passes outward, each shell tends to reach the outline of its inner gradational variant at a slightly smaller size (length). It will therefore be apparent that if size (length) remains approximately constant throughout these series, then not only has there been increase or decrease in certain dimensions with respect to length, that is to say differential growth of the shell; there also has apparently been differential growth in the same direction in any one series, but at progressively different rates according to the distance of the shell from the norm.

In fact, outward from the norm of fig. 2 there is usually a very slight increase in size, which becomes more marked towards the periphery. This increase is not great enough to suggest that the more extreme varieties shown could have grown from the penultimate and antipenultimate gradational variants without further change in the postulated differential growth rate; but it may possibly reflect phenomena similar to those recently discovered in *Carbonicola exorrecta* Eagar, a fauna of the large shell group, in which there appears to have been a falling off in the rate of increase of the H/L ratio in the latest stages of growth.

My immediate purpose, however, is merely to demonstrate that the variation diagram can reveal what appears to be differential growth in assemblages, not only in different directions but also at different rates within those directions. Thus although the general trend of relative growth in a community such as is illustrated by figs. 11a and b is at once apparent, relative growth was evidently not entirely in the same direction throughout these communities and undoubtedly took place at different rates*. The point seems of significance in interpreting statistical data, such as are shown in fig. 7. The lines drawn on this graph represent the mean growth or mass curves only. The pictograph with its complementary distribution diagram (fig. 11), arrangements into which an admittedly subjective element must enter, do nevertheless demonstrate the approximate distribution of the more

* See also the growth stages of individual shells, shown in figs. 8a and b, p. 160.

obviously different relative rates of growth, and are therefore of some value in interpreting and even in supplementing the statistical data.

MEASURED GROWTH.

(a) *Some Results on Certain Recent Shells.*

The measurement of samples of shells taken from communities of recent lamellibranchs has generally indicated more or less regular mean growth. A linear relationship between the logarithms of shell height and length

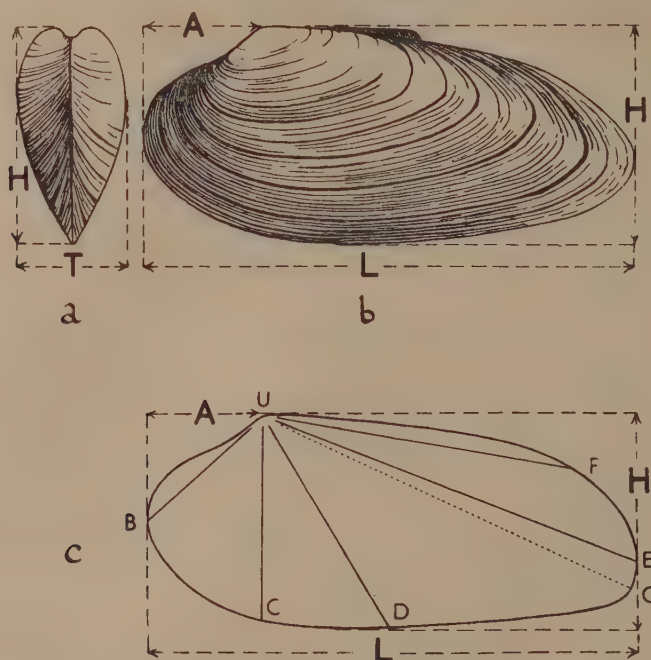


FIG. 4.—Methods of measuring a lamellibranch shell. (a) and (b) anterior and lateral view respectively to show the standard method of measuring length (L), parallel to the line of hinge. H=height, A=length of anterior end, T=thickness or obesity. In (c) UC is the distance from the umbo to the ventral margin, measured parallel to H (=v of Leitch, 1940). D is the middle point of the ventral margin measured parallel to L, and the point F lies on the postero-dorsal margin at three-quarters of the height, measured parallel to H. UG is the line of maximum growth measured from the umbo (=d of Deleers & Pastiels, 1947, figs. 1, 3).

[(a) and (b) by permission of the Royal Society of Edinburgh.]

(allometry*) has been demonstrated in the growth of several species of *Sphaerium* and in certain non-marine gastropods (Nomura, 1926 a, b). Hamai 1934 a, b, 1935, 1936, 1937) found similar results in certain species of the

* In the allometry equation, $y = bx^\alpha$, y is the part and x the whole (or standard) of the organism. α is termed the equilibrium constant of relative growth and b the initial index, that is the value of y when $x=1$ (Huxley & Teissier, 1936). This equation may be written in the form $\log y = \log b + \alpha \log x$, which is that of the growth equations written on p. 157. Thus the results of Alkins (1921), who found a linear relationship (geometric growth) between the height and length of a sample of *Unio pictorum* L., can be interpreted as a special case of the application of the allometry equation where the equilibrium constant, α , has the value of unity.

genera *Cyclina*, *Gomphina*, *Meretrix* and *Solen*. In the case of the first-named genus growth in the directions *UB*, *UC*, *UD*, *UE* and *UF* of fig. 4c showed allometric relationships both with shell length and with one another. These results suggest the possibility of using radial measurement to express some of the more subtle trends of relative growth indicated by study of the variation diagram. Further results of the work of Hamai are referred to in the succeeding section.

(b) *Carboniferous Non-Marine Shells.*

Although a number of workers have noted changes in shape with the growth of shells of the fossil family Anthracosiidae (Hind, 1894; Clift & Trueman, 1929; Dix & Trueman, 1931; Barker & Leitch, 1947), until very recently there have been no attempts to separate or define units of classification by measured growth.

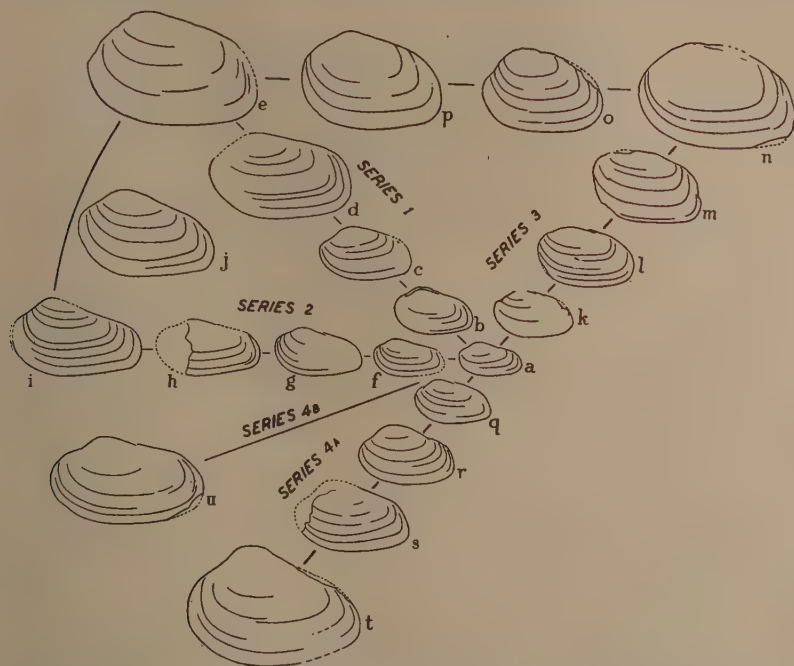


FIG. 5.—Shells from above the Sand Rock Mine (see fig. 1) collected from a small area west of Wigan and arranged in a variation diagram. The shell figured as (i) is the holotype of *Carbonicola exporrecta* Eagar, an extreme variety after which the group is named. Note that the series reveal some of the changes of shape which take place with growth. Shells $\times \frac{1}{2}$.

[By permission of the Geological Society of London.]

(i) *Fauna of the Sand Rock Mine: Allometric Growth.*

The writer was recently confronted with the separation of what appeared to be two groups of shells in the fauna above the Sand Rock Mine of the Lancashire Millstone Grit (fig. 1) over a small area west of Wigan (Eagar, 1952 d). At the main section investigated, Upholland Station Cutting (Locality 1 of fig. 8), large shells of the *Carbonicola exporrecta* group (fig. 5) were found almost throughout four feet of light grey shaly mudstone, in which

there were also four thin leaves of very small shells, a number of which showed expansion to the posterior, that is *Anthraconaia*-like outline. A plot of height of shell against length over a very wide range in size (fig. 6) suggested the possibility that the latter might be the young of the large shell group; although progressive increase in the H/L ratio of these large shells, indicated by the upward curvature of the path of points, concave to the ordinate, H , contrasts with the almost straight path of the small shells, which proves to be slightly convex to the ordinate. Fig. 7 shows the result of measuring a number of early growth lines of individuals in the large shell group and of plotting the measurements of these, with the remainder shown on fig. 6, on the double

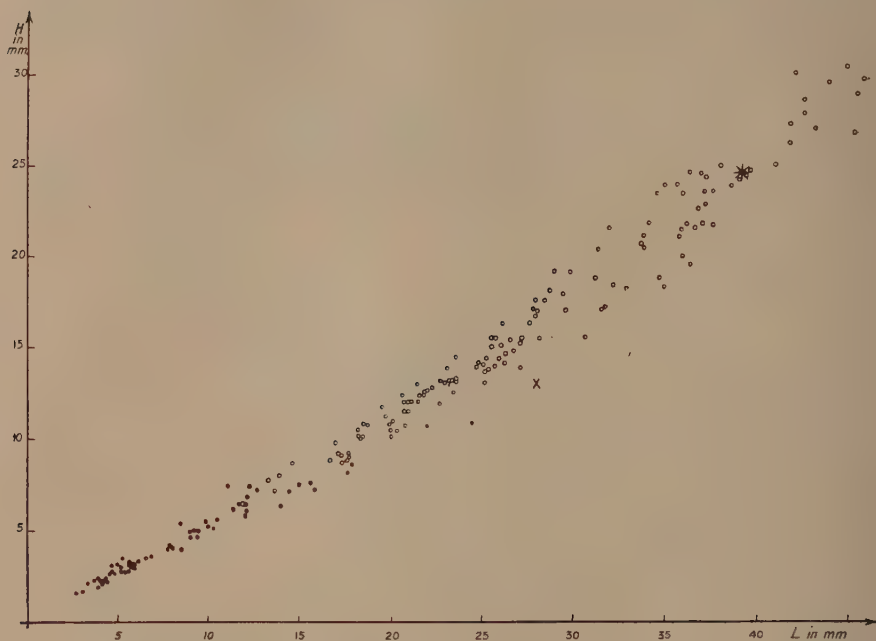


FIG. 6.—Measurements of height plotted against length for shells from above the Sand Rock Mine, west of Wigan. Note the very wide range in size. • = small *Carbonicola* ? sp. from thin leaves in the band. ○ = *Carbonicola exprorecta* Eagar, including the holotype, marked *. × shows the position which would be occupied by the holotype of *Carbonicola* ? *lenisulcata* (Trueman), from above the Pot Clay Coal, Huddersfield.

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logarithmic grid. The resultant two straight paths of dots suggest allometry with respect to the height and length of the assemblage. Using the method of least squares* (Simpson & Rowe, 1939, p. 265) we find the lines of regression

* These calculations were completed before the publication of a method of line fitting by Kermack & Haldane (1950) which avoids making one variate dependent. This method is now being used and more shells are being collected at several horizons. Results are not available at the time of going to press, but it should be stressed that it is unlikely that any of the statistical conclusions expressed here will be appreciably affected by the revisionary work.

of $\log H$ on $\log L$ are given by the following equations :

$$\log H = 1.210 \log L - 0.549 \quad (i)$$

for the large shells of the *C. exporrecta* group (fig. 5), and

$$\log H = 0.922 \log L - 0.203 \quad (ii)$$

for the remainder, the small shells.

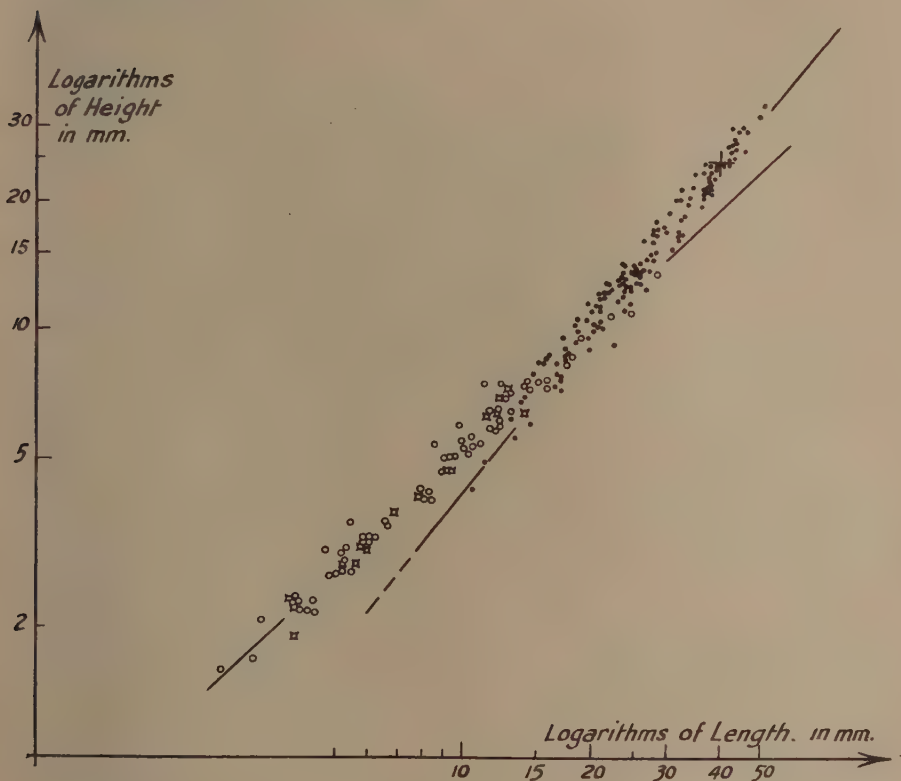


FIG. 7.—A plot of logarithms of height and length measurements of shells from above the Sand Rock Mine, to show allometric growth of two species.

• = Fauna of *Carbonicola exporrecta* Eagar, including the growth stages of 17 specimens from Mountain Mine Colliery, Upholland.

○ = Very small shells, from thin leaves in 4-foot band at a nearby section.
□ = Very small shells collected before the thin leaves were discovered, and subsequently separated from *C. exporrecta* by eye.

Lines of regression of $\log H$ on $\log L$ are drawn for each group (see above, equations (i) and (ii)). Compare with fig. 6, in which symbols for the groups are interchanged.

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The difference in slopes is highly significant, indicating in the former case a considerable increase in the H/L ratio with growth and in the latter case a slight decrease*.

* For a full discussion and further evidence for the separation of these two groups see Eagar (1952 d, p. 354).

(ii) *Allometric Growth on Higher Horizons.*

The Pot Clay Coal: Six Inch Mine.—This coal, which succeeds the Sand Rock Mine and is found over a wide area in the Pennine coalfields (fig. 1), is overlain locally in the Sheffield district by a thin leaf of large shells (Eagar, 1953, fig. 4). The fauna shows characters suggesting that it is transitional between that of *Carbonicola exporrecta* (fig. 5) and that of *C. protea* (fig. 3) of the succeeding Soft Bed-Bassy Mine succession. As far as can be ascertained from the limited material available, the shells grew with increase in *H/L* ratio at the same rates as those of *C. exporrecta*.

A statistical study of the small shell group, in which *Anthraconaia*-like outline predominates (fig. 9a) throughout the main band (fig. 1, arrows) in Yorkshire and Lancashire, indicates that growth took place with slight allometric decrease in the H/L ratio, at a rate not significantly different from that of the small shell fauna above the Sand Rock Mine. Using the common slope we have:

$$\log H = 0.917 \log L - 0.277 \quad \text{. (iii)}$$

for 71 specimens from Midhopestones, near Sheffield; and

$$\log H = 0.917 \log L - 0.198 \quad . \quad . \quad . \quad . \quad (iv)$$

for the small shells above the Sand Rock Mine (fig. 7). These equations reveal, however, a highly significant difference in the displacement of the lines (see Eagar, 1953, fig. 4). In this connection it seems worth noting that the lithology of the two bands is quite different. Some evidence for the association of changes in environment with displacement of fitted lines of allometric growth is briefly reviewed in the succeeding section (p. 159).

The Soft Bed-Bassy Mine.—In a thick series of fossiliferous beds above this coal (fig. 1), lithology and shell shape both vary greatly. The succession, moreover, is complicated by the migration of faunas and probably also by their evolution (p. 169). Work on allometric growth is far from complete; more material is required and results are as yet tentative. It may possibly be significant, however, that samples of two dominantly *Anthraconaia*-like faunas immediately succeeding pene-marine (*Lingula*) bands at Honley, near Huddersfield (see figs. 1 and 10), as far as the limited material allowed, showed the same pattern of growth as that indicated by equation (iii), above. Moreover, two highly variable shell faunas, which appeared partly intermediate between the small and large shell groups and were found in medium-grained measures near the middle of the Honley succession (fig. 10a), proved to have the following fitted lines :—

$$\log H = 1.194 \log L - 0.636 \quad . \quad . \quad . \quad . \quad (v)$$

for 32 shells collected from 13 ft. 3 in. to 13 ft. 9 in. above the coal; and

$$\log H = 1.188 \log L - 0.627 \quad , \quad . \quad . \quad . \quad . \quad (vi)$$

for 37 shells from 13 ft. 9 in. to 14 ft. 9 in. above the coal. These lines do not differ significantly between each other either in slope or in displacement. But it is interesting to note that the slope of these lines is not significantly different from that of equation (i), representing the large shell group. In other words allometric investigation of non-marine faunas with respect to height and length of shell, within the strata shown on fig. 1 (which contain the mostly highly variable faunas known in the British Coal Measures) has not yet revealed slopes of fitted lines which are significantly different from those of equations (i) and (ii) (p. 157). It must be stressed, however, that many more shells must be measured and more work must be done on early stages in the development of the Anthracosiidæ before these equations can be utilized as criteria in the recognition and definition of the two groups of shells discussed above. They are empirical formulae and must now be

considered in relation to the growth of both local communities and individual shells, and in the light of the past ecology and the systematics of these highly variable faunas.

(iii) *A Summary of the Results of Further Work on the Fauna of the Sand Rock Mine.*

Faunas on this horizon were investigated separately in the following four localities: 1, Upholland Station Cutting; 2, Beechwood Colliery, Harrock Hill; 3, Pimbo Lane Colliery (abandoned); and (4) Mountain Mine Colliery (abandoned). Localities 1, 3 and 4 lie within a mile of one another at Upholland, 4 miles west of Wigan. Locality 2 lies $4\frac{1}{2}$ miles to the north of Upholland.

(a) *Changes in the growth rate towards old age.*—At localities 2, 3 and 4, where it was possible to measure the growth lines ("young stages"*) of faunas of *C. exporrecta*, the rate of increase in the H/L showed a sudden decline at about two-thirds of the local maximum length of the shell. The change of slope of the fitted line, from 1.210 to 1.074 was found to be the same in the three localities investigated. It is interesting to note that Hamai (1937), plotting the logarithms of shell height and length in a recent species of the marine genus *Meretrix*, found a similar inflexion and falling off in the rate of increase of the H/L ratio at about two-thirds of the maximum shell length.

(b) *The effects of allometric growth and absolute size in local faunas.*—Since shells show progressive changes in shape with growth, faunas of smaller size may have a distinctly different appearance from those in which growth has proceeded to a larger size; and such faunas might previously have been assigned to different species. In spite of the old-age effect described above and of further complications (item (d) below) it is worth noting that a reduction of a mean length of 37.8 mm. for 33 specimens from locality 4, to 22.2 mm. for 50 specimens from locality 1, caused decrease in the mean H/L ratio from 62.9 per cent to 54.1 per cent and in the mean A/L ratio from 28.8 per cent to 25.3 per cent. The ranges of these ratios were also considerably altered (see Eagar, 1952 d, fig. 7).

(c) *The growth of individual shells.*—In fig. 8a and b, H/L ratio of shell is plotted against length and the young stages of a few typical individuals are joined together. Although there is some evidence that the individual rate of increase of the H/L ratio tended to fall off in the later stages of growth, the lines mainly emphasize the point brought out by the variation diagrams, the existence of different rates of relative growth within the mass allometric curve.

(d) *Relative growth rates and sedimentation.*—Strong evidence has been adduced to suggest that progressively heavier sedimentation took place through the localities 4 to 1, that is in their reverse numerical order (Eagar, 1952 d, p. 359 *et seq.*). The shells are reduced in size in this direction and at the same time tend to show progressively steeper lines of growth, the more elongate forms being eliminated (fig. 8b, a). The writer's interpretation of the evidence, which implies stunting, a slight alteration in relative growth rates with decrease in size, is summarized in fig. 8c. The allometric lines of mean growth of these faunas, both for young stages and adults, are significantly displaced, but their slopes are not affected. In this connection it is interesting to note that Hamai (1937) found that environmental differences were reflected in the allometric growth of the freshwater *Sphaerium heterodon* (Lea). The line of mean growth was displaced when the fauna was traced into a different environment, but the slope remained unaltered. Similar results on the relative height of shore limpets are well known.

* In the following summary and in the description of fig. 8 "young stages" denotes the measurements of growth lines of the shells. The word "adults" is reserved for measurements to the shell margins, irrespective of the size of the shells.

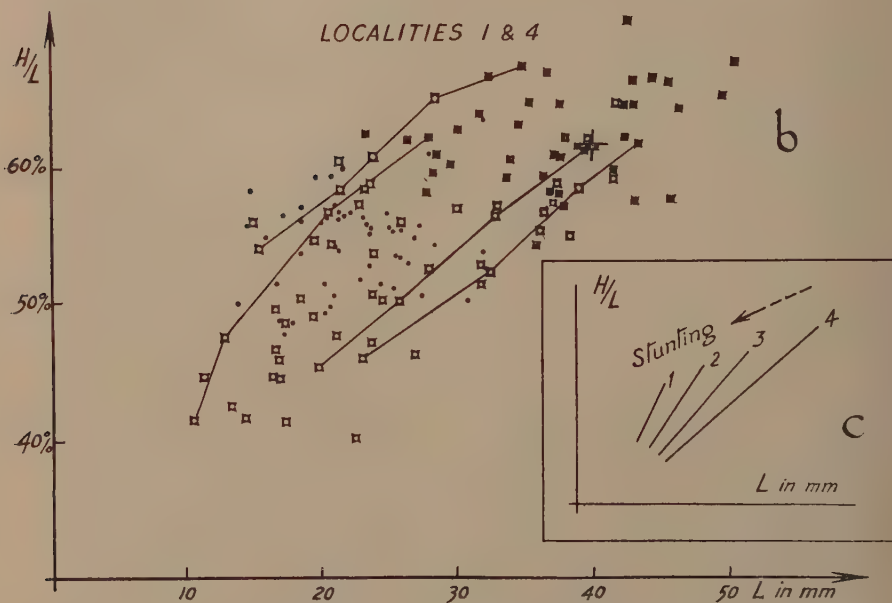
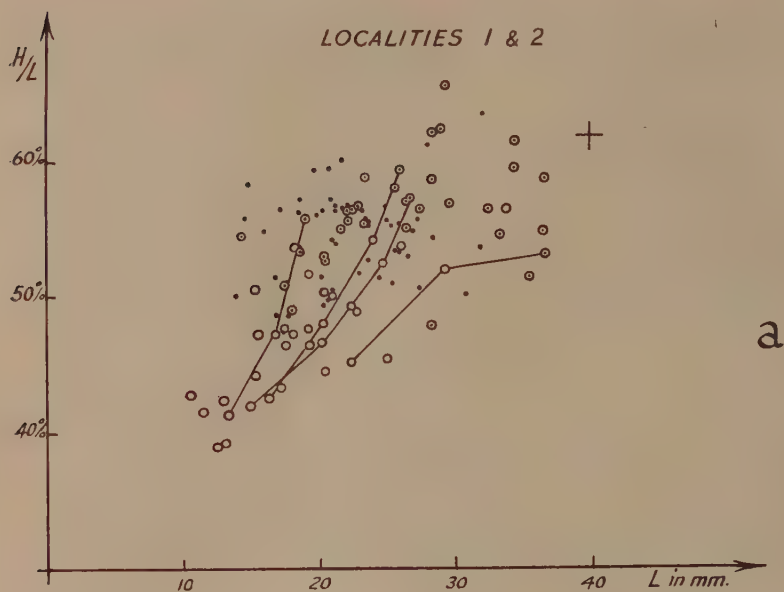


Fig. 8 (a) and (b). Height/length ratio of shell plotted against length to illustrate changes in the ratio with growth in faunas of *Carbonicola exposita* above the Sand Rock Mine at four localities west of Wigan (see p. 159). Symbols denote: Locality 1, •=adults (see p. 159); Locality 2 (Harrock Hill), ○=adults, ○=young stages; (For continuation of legend see opposite page.)

RELATIVE GROWTH AND ENVIRONMENTAL CHANGE.

(a) *Results from the Main Band above the Pot Clay Coal-Six Inch Mine.*

The main band above this coal (fig. 1, arrows) yields the small shell fauna, briefly referred to on p. 158, containing *Carbonicola* ? *lenisulcata** (Trueman), *C.* ? aff. *bellula* (Wright) and *C.* ? aff. *fallax*. In Yorkshire the fauna has been traced from Huddersfield to Sheffield and across the Pennines to the western margin of the Lancashire Coalfield. The fauna was examined throughout the area where the band is found and detailed studies were made at four localities in each of which slightly different environmental conditions appear to have obtained:—1, Midhopestones, near Sheffield; 2, Darwen Hill, four miles south of Blackburn; 3, Wrightington; and 4, Middlehurst Wood. The last two localities lie two miles apart and approximately six miles north-west of Wigan. The main results may be very briefly summarized:

(i) Slight differences in the displacement of the line of mean allometric growth of shell height and length were doubtfully significant between localities 1 and 2 and not significant between the remaining localities.

(ii) The faunas throughout the area tended to grow from *Carbonicola*-like forms (with very approximately oval outline) to more elongate shells in which the posterior end tended to be expanded and elongated (*Anthraconaia*-like outline). The same tendencies were noted in the growth of the small shell fauna above the Sand Rock Mine.

(iii) Evidence was adduced for considering that sedimentation was least in locality 1 and heaviest in localities 3 and 4. An appreciable decrease in size (length) at the latter two localities has contributed, by reason of the mode of growth of the fauna (item (ii) above) to the increased proportion of *Carbonicola*-like forms they display (fig. 9a, see numerical increase in the northern series towards locality 4 and refer to fig. 2).

(iv) That the above changes are not merely due to decreased size may be seen by comparing the diagrams of localities 1 and 2, between which there is an *increase* in size.

(v) When changes in the faunas due to differences in size are excluded, and when allowance has been made for the effects of lateral crushing in some of the specimens (p. 150), it is clear that certain changes in the faunas accompany

* This tentative generic revision (from *Anthraconaia*) is discussed by Eagar (1952 d, p. 367; 1953, p. 164). The mark of interrogation denotes the fact that although internal as well as external features of the shell on succeeding horizons suggest that the group belongs to the genus *Carbonicola* rather than *Anthraconaia*, no internal features have been seen on this horizon, from which the type of *Anthraconaia lenisulcata* was obtained.

Locality 4, □=adults, ■=young stages. (Shells from Locality 3 are not shown. The points lie approximately over the area covered by those of Localities 2 and 4.) + =holotype of *C. exprorecta*.

The shells whose growth is illustrated by joined stages have been selected as typical. In the case of the fauna from Locality 4, lines joining stages tended to segregate into two groups with higher and lower *H/L* ratios. It is just possible that these may represent male and female shells.

Note the general steepening of the lines of growth, illustrated or implied, as one passes from Locality 4 through 2, to 1. A simplified representation of the author's interpretation of the data is shown in (c), inset, where the lines 1 to 4 should be regarded as very approximately representing the modal growth of faunas from Localities 1-4 respectively.

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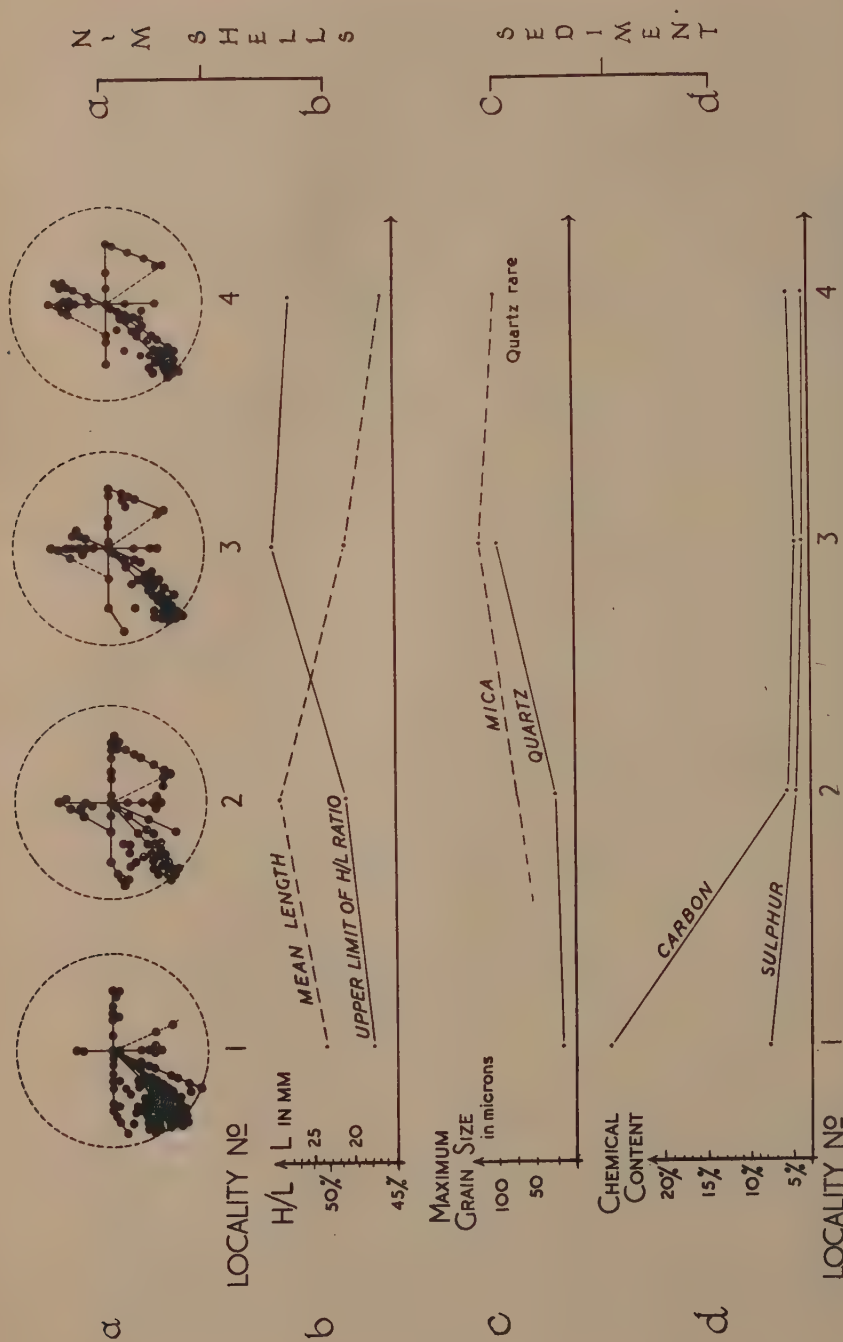


Fig. 9.—A summary of faunal and lithological changes in the main non-marine shell band above the Pot Clay Six Inch Mine through four localities ranging from Midhopestones, near Sheffield (1), to Wrightington (3) and (4), north-west of Wigan (see p. 161). (a) Distribution diagrams, in which each small black circle represents the position of a shell, based on the arrangement shown in the Standard Diagram (fig. 2). (b) Some changes in shell dimensions. (c) Maximum sizes of the main detrital constituents of the fossiliferous shale and shaly mudstone. (d) Some data from a chemical analysis of the same shales and shaly mudstones.

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increased coarseness in the grain size of the fossiliferous shale, reflecting increased water velocity of the habitat*. These changes, again, may be summarized :

- (a) The fauna is dominantly *Anthraconaia*-like in outline in fine-grained richly carbonaceous and pyritous shales (fig. 9a, c, d, locality 1), where ventral margins of the shells tend to be rounded (west and south-west series of fig. 9a, locality 1).
- (b) With passage into more coarsely grained and ferruginous sediments the faunas become more variable; the upper limits of the H/L and A/L ratios are increased (fig. 9b) and there is a small significant increase in the mean H/L and A/L ratios between localities 1 and 2. These changes are seen in the variation diagrams in the proportion of *Carbonicola*-like forms with relatively large H/L ratio, which increase at the expense of the more elongate *Anthraconaia*-like forms.
- (c) With increasing coarseness of grade size in the sediment there is a tendency for ventral margins of shells to be straightened. This is seen in a slight shift in numbers from west to east and south-east in the distribution diagrams.

(vi) Some results of work on the ecology of recent European and North American Unionidae (summarized by Eagar, 1948) reveal certain morphological tendencies and dimensional changes in the shell which appear to be correlated with differences in the relative water velocity† of the habitat. These results parallel those of items (ii) a, b and c above and certain conclusions based on the study of the succeeding Soft Bed-Bassy Mine succession (items (2b, c), p. 165).

- (a) Expansion of the posterior end of the shell, often with the development of a long hinge line, appears to be characteristic of lake forms or those living in relatively slowly moving water. This tendency has been seen in varieties of a single species.
- (b) In general the H/L ratio of shells may vary considerably according to environment. With increase in water velocity both increase and decrease of the H/L ratio of the shell has been observed in different species.
- (c) Curved ventral margins also *tend* to be characteristic of slowly moving water, downstream or lake environments, whereas a relatively high water velocity or an upstream environment tends to be associated with shells having a straight or reflected ventral margin (Eagar, 1948, p. 146).

(b) *The Soft Bed-Bassy Mine Succession.*

(i) *Introduction.*

Much has recently been published on the succession (Eagar, 1947, 1948, 1951, 1952 a). It is sufficient merely to state here that the beds (fig. 10) show three small-scale incomplete examples of cycles of sedimentation such as are typical of the Upper Millstone Grit and Lower Coal Measures of the Pennine region, where such a unit passes upward from fossiliferous to barren shale

* The evidence for shell growth *in situ* is overwhelming in nearly all cases in the faunas under discussion. Nevertheless the possibility that some material occasionally has drifted has not been overlooked in evaluating results. See R. M. MacLennan (1945), "Generations in a Fossil Community".

† It is, of course, realized that such a factor as water velocity involves many others, all of which may under certain circumstances show some correlation with the size of the stream and the movement of the water, or may act as more or less independent variables.

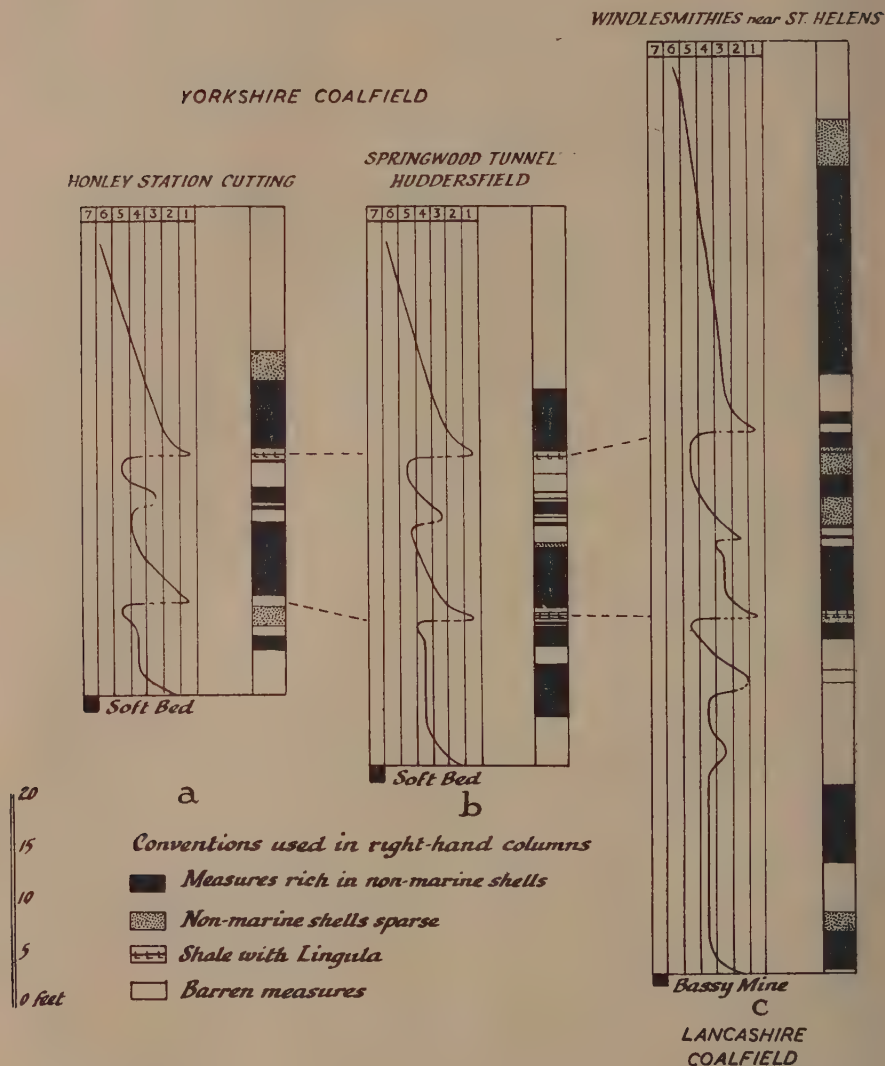


FIG. 10.—Sections of measures above the Soft Bed-Bassy Mine showing (left) lithological variation and (right) details of non-marine shell bands. The numbers on the grids refer to selected lithological grades, fully described by Eagar (1947, p. 12). Grade 1 represents fine-grained strongly pyritous shale (probably of marine origin), Grade 2 fine-grained carbonaceous and ferruginous shale, and the remaining numbers progressively more coarsely grained sediments ranging up to siltstone (Grade 5). Grade 6 represents more coarsely grained sediments including sandstone and grit, and Grade 7 coal. The sediment is placed in the appropriate column and a line is substituted for the blocks in such a manner as to give the shale grade continuously throughout the sections.

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and shaly mudstone, showing gradual coarsening in grain size, to sandstone, fireclay and coal seam. The coal is overlain by a marine or non-marine shell band commencing the succeeding cycle. Such cyclic units, or cyclotherms, preserve their identity over very wide areas in the Coal Measures, where conditions were remarkably uniform (Trueman, 1946), and indicate a recurrent series of changes to which the depositional area, or 'delta' was continually subject. Marine or relatively open water conditions were succeeded by a shallower and more variable 'up-river' environment in which the water moved more swiftly, to be followed by silting up, and the growth of sand banks over which coal forests ultimately spread. The cycles frequently fail to reach the last episode but their general trend is unmistakable. The Soft Bed-Bassy Mine succession provides a unique opportunity for the ecological study of non-marine shells, since they are found closely following pene-marine (*Lingula*) bands (fig. 10) and extend through a considerable thickness of the cyclic unit, and thus into conditions changing in a known direction, the trend of which is illustrated by the method of plotting lithology shown in fig. 10.

(ii) *A Summary of Some Results.*

1. In general, variation was much reduced as progressively smaller thicknesses were collected (e.g. fig. 11*b*). Some thin bands, however (e.g. fig. 11*a*), still showed a remarkable range of variation.

2. When traced upward through each cycle, the faunas passed through the same sequence of changes.

- (a) The small shell group occurs at the base of each cycle. The large shell group, of *C. protea*, is found in coarser grained measures and is found exclusively, with a distinctive pattern of variation, at the top of the lower and middle cyclic units.
- (b) Faunas at the base of the cyclic units and probably therefore of lamellibranchs which lived in the most nearly marine, or open water, conditions, and in relatively the most slowly moving water, appear closely similar to the small shell faunas of the preceding horizon of the Pot Clay Coal-Six Inch Mine, especially to the fauna of locality 1 (fig. 9*a*), where the fossiliferous shale is of similar fine grain and equally rich in carbonaceous matter.
- (c) As one passes from the base to the lower and middle parts of the cyclic units the shells become progressively more variable and undergo changes which are essentially those seen in the main band above the Pot Clay Coal-Six Inch Mine, as it is traced into more coarsely grained measures. But the changes on these higher horizons proceed much further, some of them within a few inches upward from the base of the cyclic units, where there is little change in the grade of the sediment (see fig. 10). Thus an *Anthraconaia*-like fauna at the base of the upper cyclic unit at Honley (fig. 11*c*) within nine inches changes to one almost entirely of *Carbonicola* (fig. 11*d*), although within this interval the change takes place gradually. Other upward changes within the cycles include increases in size, in *H/L* and *A/L* ratios and in a tendency for the ventral margin to become straight or reflected, just as was noted in the faunas of the Pot Clay Coal-Six Inch Mine.
- (d) In spite of these parallel changes, the faunas of each cyclic unit are recognizable as a whole and on certain horizons, notably near the tops of the units, contain distinctive faunas (e.g. *C. haberghamensis* Wright (fig. 11*a*) and *C. discus* Eagar. These faunas are easily

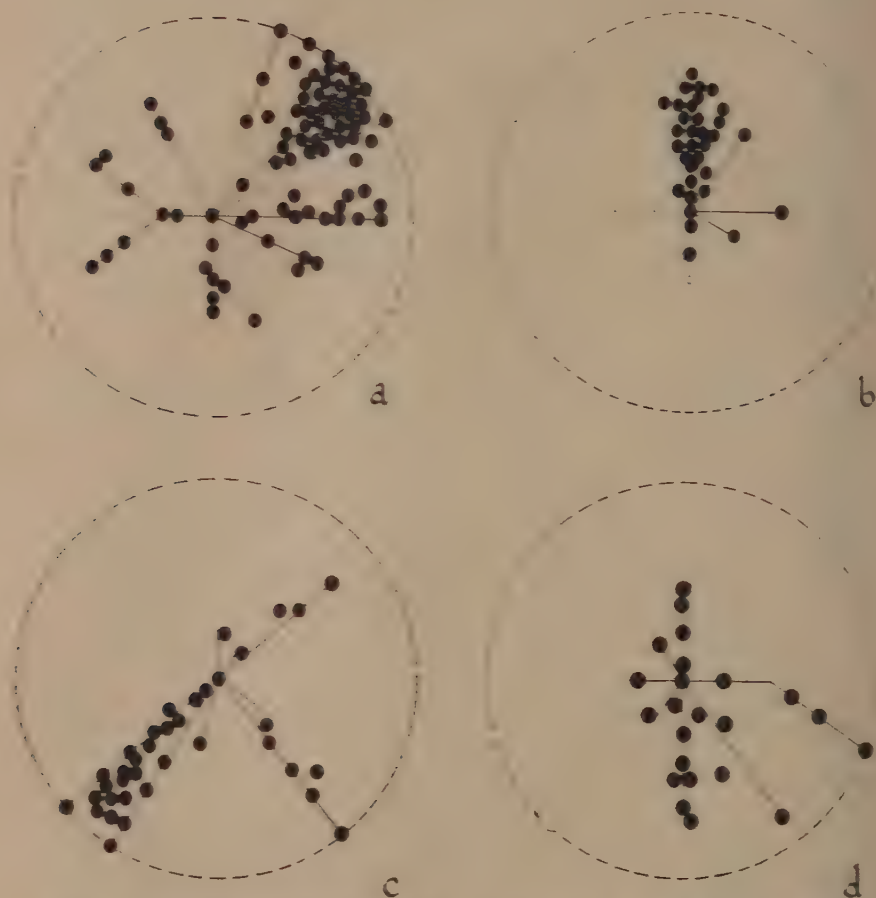


FIG. 11.—Dumbleton diagrams based on the plan shown by the Standard Diagram (figs 1 and 2) of shells across the Soft Bed Coal at Hemley near Rinderfield, Yorks. Each small black circle represents the position of one shell.

a. Fauna of *Cardium* *halimoides* (19 ft. 9 in. to 21 ft. above the coal, showing considerable variation—C. planus diagram, fig. 3).

b. Fauna of *Cardium* *aff. swops* (Eagar MS., 19 ft. 6 in. above the coal, showing very limited variation and a steep increase in H/L ratio with growth—C. planus diagram fig. 2 (see also fig. 11 c)).

c. Fauna of *Ammonia*-like shells (*Cardium* *aff. swops* 19 ft. 3 in. above the coal at the base of the upper spout unit—see fig. 10. C. planus diagram).

d. Fauna of elongate *Cardium* *aff. planus* and *C. aff. swops* (Eagar MS., from 5 in. above the horizon of c.). Note the complete change in the fauna between these two horizons.

[After figures published by the Royal Society of London.]

recognizable over nearly the whole Pennine area, and are not repeated*. Thus, although there are many obviously ecological changes, it appears that the shells also were evolving.

- d. What appear to be species splits may be traced in the middle and upper parts of cyclic units (fig. 12) where true species, separated by their different modes of relative growth, evidently lived together. Compare in order figs. 12a, b and c, where the small shell group is

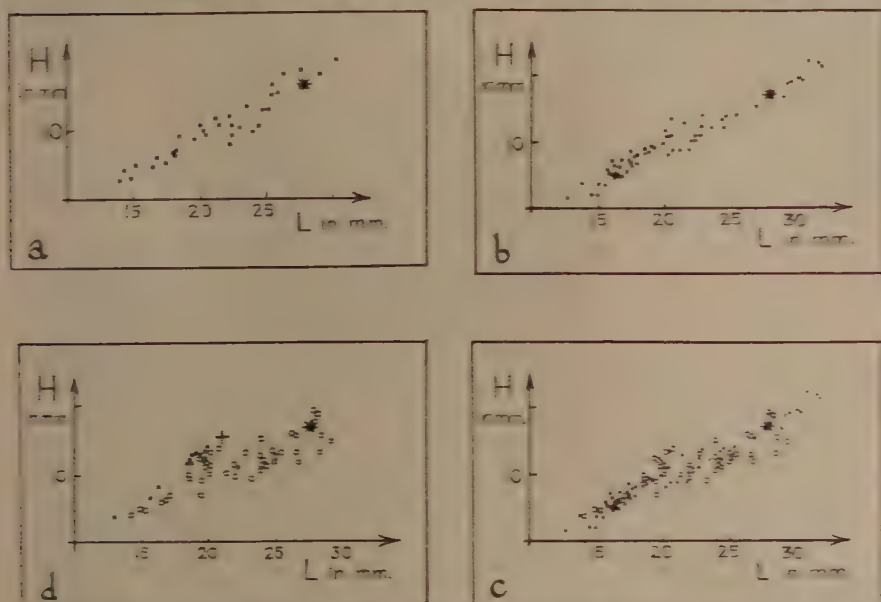


FIG. 12.—Splitting and apparent speciation revealed in plots of shell height against length.

(a) Fauna of *Carbonosia fallax* Wright, from the lower cyclic unit of the Soft Bed-Basely Mine succession, 10 ft. in. above low water at Fenscowles, near Blackburn, Lancs.

(b) Fauna of *Carbonosia fallax*, with second smaller fauna, growing with steeper increase in H/L ratio and referable to *C. cf. crispa* Eagar MS., from Fenscowles, 3 in. to 6 in. above the horizon of (a).

(c) Small black dots show the same fauna as in (b) above. Small circles show the dimensions of two distinct species found in thin leaves 6 in. apart near the top of the middle cyclic unit of the succession at Honley: the larger group referable to *Carbonosia fallax* with more elongate varieties assigned to *C. scripta* Eagar MS.; the smaller group, with steep increase in the H/L ratio, is again *C. cf. crispa*.

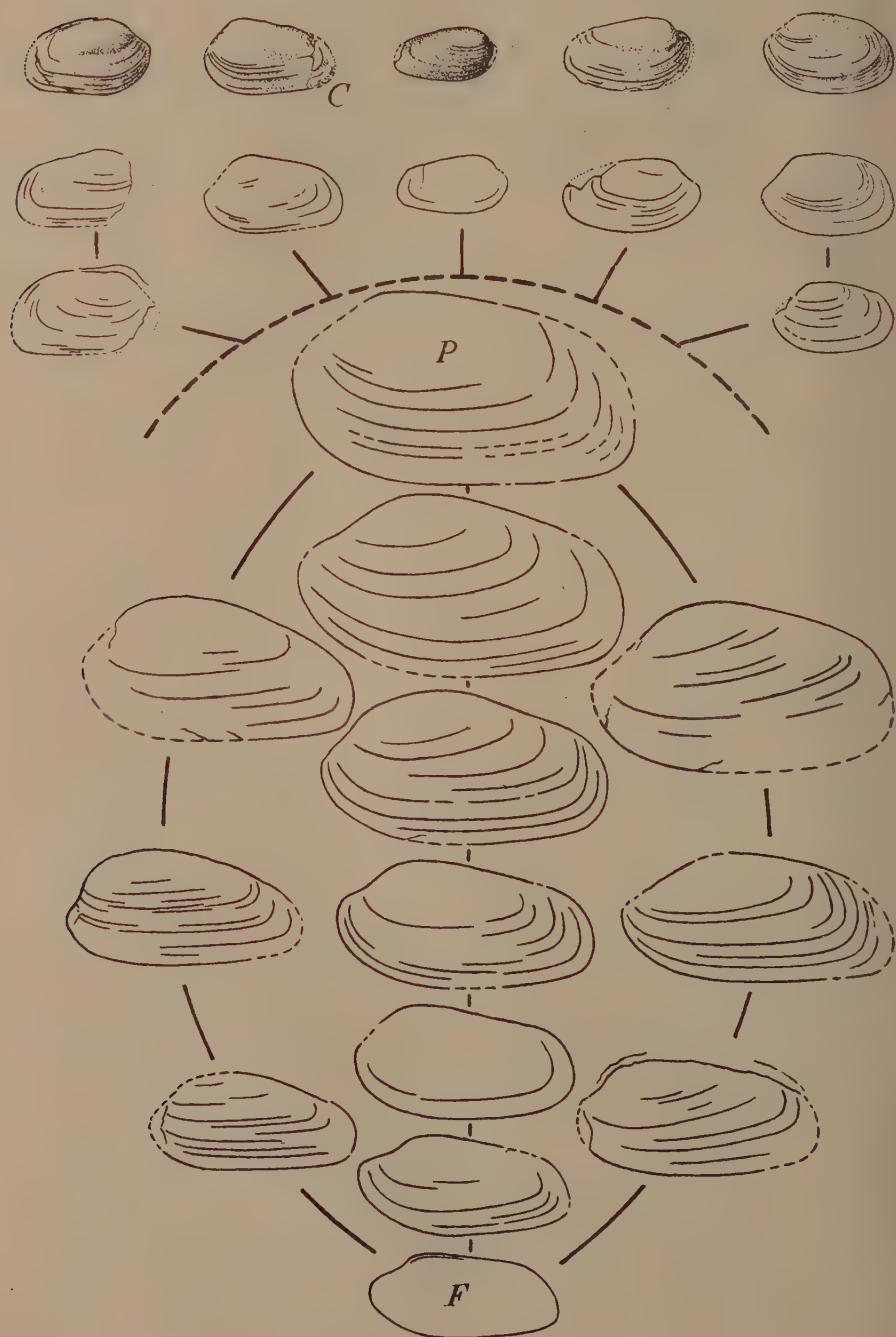
(d) Small circles indicate the same two faunas as are portrayed in (c) right. Dots indicate the measurements of a fauna of *C. crispa* from above the horizon of the 80 Yards Coal at Sander Chemical Works bore-hole, Bradford, 150 ft. above the Soft Bed Coal.

* = Holotype of *C. fallax* Wright. + = Holotype of *C. crispa*, Eagar MS.

[a], [b] and [c] by permission of Manchester Geological Association and Liverpool Geological Society.]

seen dividing into a smaller subgroup with steeper increase in H/L ratio than occurs in *C. fallax*, which clearly belongs to the larger subgroup. Whether this split is merely being repeated in the middle cyclic unit (fig. 12c, small circles), or whether it is the same split, further accentuated by time and migration, is not at present

* I have hammered through nineteen almost complete sections of these measures throughout Lancashire and Yorkshire, inch by inch, collecting extensively.



[For legend see opposite page.]

clear. The two groups are dimensionally further apart in the middle unit and their behaviour on these horizons makes a contribution towards the interpretation of a group of small shells (fig. 13, top row) first found above the horizon of the 80 Yards Coal at Bradford, some 250 feet above the Soft Bed. This fauna was referred to '*C. protea* (small form)'. And indeed all the original variants found with it may be more or less closely matched with selected variants of *C. protea*, reduced to half size (fig. 13, second and third rows of shells). Below these in fig. 13, however, are shown growth series from the Soft Bed-Bassy Mine succession leading to *C. protea*, all at natural size. It should be clear from the comparison that the relative rates of growth of the two groups of shells are entirely different, and that the rate of increase in the *H/L* ratio with growth is *much* larger in the smaller group. In fact the true systematic position of *C. crispa* should probably be sought by reference to figs. 12*a-d*, in which its measurements merely suggest that the fauna belongs to that of fig. 12*b* (smaller group) which, on this higher horizon, has become further differentiated.

(iii) *The Interpretation of Faunal Changes.*

The Soft Bed-Bassy Mine succession is complicated by a number of independent factors, many of which we cannot determine with the methods of investigation available at present. If we consider changes only in the non-marine shell fauna, then these are probably a combination of three kinds.

First come changes due to migration, of which undoubted examples appear to be the arrival of identical faunas of *Carbonicola protea* at the extreme top of the lower and middle cyclic units of these measures. Migration doubtless played some part in other generalized changes in the variation which take place in the the same order in each unit.

Secondly there may have been changes due to phenotypic modification, that is the effect of external environmental conditions. We have some reason to suspect that this type of modification has taken place, since it is widespread among recent freshwater Unionidae. Some morphological tendencies in this family, which appear in response to differences in water velocity, may be seen also in certain groups of the Anthracosiidae, where they appear to be correlated with the same differences in relative speed of water (item (vi), p. 163), as far as this is revealed by the lithology of the fossiliferous sediment. As has been clearly shown by Joysey (1952), progressive change in the distribution of a series of geographical subspecies could give the appearance of continuous evolution in any one section; while phenotypic modification could considerably increase the range of variation at points in the succession where conditions have been periodically variable and deposition slow. Since the above factors may influence, to a greater or smaller extent, the succession of measurable

FIG. 13.—Top row of shells: *Carbonicola crispa*, Eagar MS. (C) and associated varieties from above the horizon of the 80 Yards Coal at Sandoz Chemical Works bore-hole, Bradford, Yorkshire. Natural size.

Second and third rows: outlines of selected varieties of a fauna of *Carbonicola protea* Wright from the lower cyclic unit of the succession above the Bassy Mine at Feniscowles (250 ft. below *C. crispa* at Bradford), drawn at half natural size. Note closely similar forms beneath each variety of the *C. crispa* group.

Below the curved broken line are seen apparent growth series between *Carbonicola fallax* (F) and *C. protea* (P), all at natural size. (Young members of the *C. protea* group tend to show slightly more taper to the posterior than is found in *C. fallax* (see varieties immediately above this shell), but the diagram illustrates the difficulty of separating *C. fallax* from these apparently immature forms.)

[The lower diagram is after a figure reproduced by the Royal Society of London.]

and continuously variable communities in any one section, the theoretical difficulties involved in using relative growth as an aid to systematics are seen to be considerable. (For a further general discussion involving this topic see George, 1948, p. 39.)

There is, however, fairly strong evidence that changes of evolutionary significance, presumed to be of genetical origin, have also taken place. And in my opinion recent work on the lateral extent of the faunas of the Soft Bed-Bassy Mine succession (Egar, 1952 a) and on those of the Pot Clay Coal-Six Inch Mine has tended to emphasize the part played by such changes (Egar, 1953, p. 188). It has been suggested that the widespread faunas of *Carbonicola discus* and *C. haberghamensis* were the products of genetical change, involving in the latter case the evolution of a peri-umbonal bulge in the shell, a feature which persisted to horizons much higher than that of the middle cyclic unit of the Soft Bed-Bassy Mine succession, where it is first found. Evidence for supposed genetical changes of evolutionary significance is, in fact, accumulating as more work is done on ecological aspects of the faunas. But it is admitted that at present the focus in this work is trained on ecology and on the apparent influence of environment on the organism and its mode of growth, rather than on the subdivision of the fossil material. It seems better to understand first and to divide afterwards.

SUMMARY AND CONCLUSIONS ON RELATIVE GROWTH AND SYSTEMATICS.

The study of the relative growth of the shell is often necessary and may be important in the investigation of faunas showing wide and usually, but not invariably, continuous variation, such as may be found living in non-marine conditions. Simple plotting of the heights of shells against their lengths usually forms the starting point of such work and may, without further analysis, reveal the essential evidence required by the systematist. The separation of fossil material by this means is shown in fig. 12*b, c*.

Recent work on certain early and highly variable groups of the Anthracosidae emphasizes the inter-relationship between the variation diagram, or pictograph, on the one hand, and the measurement, graphical and statistical treatment of shells, on the other. Both methods of approach can be complementary, revealing the nature of relative growth in the community, and together emphasize the distinction between true relative growth rates in shell development, as indicated by plotting the measurements of successive growth stages in a single shell, and apparent mass growth rates, indicated by dimensional plotting of many shells and the fitting of regression lines.

Empirical formulae, defining mass growth in terms of an allometric relationship between shell height and length and expressed by equations of fitted lines, have proved useful, with other criteria, in separating two groups of shells at the top of the Millstone Grit Series (fig. 1). The same formulae play a useful part in the recognition of these two groups on higher horizons in the Lower Coal Measures, where, in the few cases so far investigated, the slopes of the fitted lines for each remained constant, differences being found only in the intercepts or displacements of the lines. Such differences may be largely of environmental significance.

Although the above results may be paralleled by very similar ones described by Japanese workers investigating the shell growth of communities of recent lamellibranchs, it is stressed that they are tentative, and must so remain until confirmed by the measurement and treatment of more material. It is particularly desirable that more work be done on the early development of the Anthracosidae, in so far as this can be traced by growth lines and immature specimens.

It seems that if rates of the relative growth of the shell are ultimately to become a tool in systematic treatment, then they must be seen in their proper perspective so that their limitations as well as their potentialities

may be understood. That environment can exert a significant influence on relative growth is now undoubted. Evidence from a study of shell growth at the top of the Millstone Grit strongly suggests that relative growth has been modified by sedimentation, causing stunting. And there is abundant evidence from several horizons that certain morphological trends in shell outline tend to be associated with differences in relative water velocity, indicated by the maximum size of the detrital components of the fossiliferous sediment. Very similar morphological tendencies, affecting relative growth and correlated with the same changes in the relative water velocity of the habitat, have been found among recent Unionidae. But it should always be remembered that past differences in ecology are not necessarily revealed by the sediment. Some of the complexities of the problem have been referred to in a brief analysis of factors involved during the deposition of the Soft Bed-Bassy Mine succession (p. 169), in which migration has also played a part.

At least there appear to be less complications in the succeeding zones of the Coal Measures, which include the main productive seams. The fauna of the Pennine Lower Coal Measures is unrivalled in the extent of its variation. During their deposition, as Leitch has suggested (1936, p. 399), non-marine lamellibranchs, and especially the Anthracosiidae, may have been undergoing an initial vigorous phase of differentiation along several lines, colonizing new environments. Subsequently some evolutionary vigour was lost, and in later faunas variations became fewer and more stereotyped "and the resulting variants continue long enough to produce useful stratigraphical indices". Thus although evolutionary changes seem to have been taking place in the Lower Coal Measures, there is, as yet, little evidence of major progressive change, such as occurs in the *Anthraconaia modiolaris-adamsi* plexus (Leitch, 1940), where Sylvester-Bradley (1951) has suggested that chronological subspecies might be utilized. In the Pennine Lower Coal Measures we are concerned not with the definition of chronological subspecies, but with the recognition of different facies and ecological subspecies. These we cannot hope to define and usually do not need to separate except as certain trend patterns in the pictograph (see McKerrow, 1952, p. 150).

The present special system of nomenclature utilized by the authors of the monograph now appearing (Trueman & Weir, 1946-1952) was fully described by Leitch (1951) and is well adapted to deal with most of the systematic difficulties which arise. But as Sylvester-Bradley has pointed out (in Eagar, 1952 b), its special use of the term "species" fails to conform to standard practice, so that under the new International Rules of Zoological Nomenclature, "species" of the Anthracosiidae can only rank, as separate entities, as members of the infra-subspecific category. If they are to be termed varieties we are then confronted with a trinomial nomenclature in which it is extremely difficult to define the second term (*ibid.*, p. 53). And until much more is known about the general succession of non-marine shells in the Carboniferous System our special use of nomenclature provides the only practical solution and must therefore remain. This, however, does not preclude the possibility that ultimately a reconciliation may be found between standard practice and the special demands of the utilitarian system we employ. We are certainly not yet in a position to use relative growth as a systematic tool, but it may be very tentatively suggested that its study and description in mathematical terms may possibly be able sometime to contribute to the problem of defining even chronological species, the second term in the suggested trinomial system.

ACKNOWLEDGMENT.

The writer would express his gratitude to Mr. A. M. Walker, of the Department of Statistics, Manchester University, for advice and assistance in statistical procedure and calculation in several instances.

REFERENCES TO LITERATURE.

- AITKEN, W. G. & MCKERROW, W. S. 1948. Rhynchonellids of the Boueti Bed of the Great Oolite Series of Langton Herring, Dorset; a Study in Variation. *Geol. Mag.*, **85**, 19-32.
- ALKINS, W. E. 1919. Notes on the Growth and Variation of *Unio pictorum* (L.). *J. Conch.*, **16**, 228-233.
- BARKER, W. R. & LEITCH, D. 1946. Fossil Plants and Non-Marine Lamellibranchs from the Newhill Mine, Wath-on-Dearne, Yorkshire. *Proc. Yorks. geol. Soc.*, **27**, 82-98.
- CLIFT, S. G. & TRUEMAN, A. E. 1929. The Sequence of Non-Marine Lamellibranchs in the Coal Measures of Nottingham and Derbyshire. *Quart. J. geol. Soc. Lond.*, **85**, 77-108.
- DAVIES, J. H. & TRUEMAN, A. E. 1927. A Revision of the Non-Marine Lamellibranchs of the Coal Measures and a Discussion of their Zonal Sequence. *Quart. J. geol. Soc. Lond.*, **83**, 210-257.
- DELEERS, C. & PASTIELS, A. 1947. Etude Biometrique des *Anthraconaia* du Houiller de la Belgique. *Ass. Etude Paléont. Strat. Houillères*, Pub. **2**, 1-99.
- DIX, E. & TRUEMAN, A. E. 1931. Some Non-Marine Lamellibranchs from the Upper Part of the Coal Measures. *Quart. J. geol. Soc. Lond.*, **87**, 180-210.
- EAGAR, R. M. C. 1947. A Study of a Non-Marine Lamellibranch Succession in the *Anthraconaia lenisulcata* Zone of the Yorkshire Coal Measures. *Phil. Trans. (B)*, **233**, 1-54.
- . 1948. Variation in Shape of Shell with respect to Ecological Station. A Review dealing with recent Unionidae and Certain Species of the Anthracosidae in Upper Carboniferous Times. *Proc. roy. Soc. Edinb. (B)*, **63**, 130-148.
- . 1951. A Revision of the Sequence and Correlation of the Lower Coal Measures West of Wigan. *Quart. J. geol. Soc. Lond.*, **107**, 23-50.
- . 1952 a. The Faunal Succession above the Soft Bed and Bassy Mine in the Pennine Region. *Lpool. Manch. geol. J.*, **1**, 23-26.
- . 1952 b. Some Problems in Invertebrate Palaeontology. Contribution to a Symposium on 'Evolutionary Trends and Classification'. *Proc. Leeds phil. Soc.*, **6**, 50-53.
- . 1952 c. A Note on the Measurement of Certain Non-Marine Shells. *Mem. Manchr. lit. phil. Soc.*, **92**, 155-160.
- . 1952 d. Growth and Variation in the Non-Marine Lamellibranch Fauna above the Sand Rock Mine of the Lancashire Millstone Grit. *Quart. J. geol. Soc. Lond.*, **107**, 339-373.
- . 1953. Variation with respect to Petrological Differences in a Thin Band of Upper Carboniferous Non-Marine Lamellibranchs. *Lpool. Manch. geol. J.*, **2** (in the press).
- GEORGE, T. N. 1948. Evolution in Fossil Communities. *Proc. R. phil. Soc. Glasg.*, **73**, 23-42.
- HAMAI, I. 1934 a. On the Local Variation in the Shells of *Meretrix meretrix* (L.) with Special Reference to the Growth of the Organism. *Sci. Rep. Tohoku Univ. (Biol.)*, **9**, 131-158.
- . 1934 b. Relation between the Weight, Volume and Linear Dimensions in *Meretrix meretrix* (L.). *Ibid.*, **9**, 205-212.
- . 1935. A Study of One Case in which Environmental Conditions produce Different Types in *Meretrix meretrix* (L.). *Ibid.*, **10**, 485-498.
- . 1936. Relative Growth in Some Bivalves. *Ibid.*, **10**, 753-765.
- . 1937. Some notes on Relative Growth, with Special Reference to the Growth of Limpets. *Ibid.*, **12**, 71-95.
- HUXLEY, J. S. & TEISSIER, G. 1936. Terminology of Relative Growth. *Nature, Lond.*, **137**, 780.
- JOYSEY, K. A. 1952. Fossil Lineages and Environmental Change. *Geol. Mag.*, **89**, 357-360.
- KERMACK, K. A. & HALDANE, J. B. S. 1950. Organic Correlation and Allometry. *Biometrika*, **37**, 30-41.
- LEITCH, D. 1936. The *Carbonicola* Fauna of the Midlothian Fifteen Foot Coal; a Study in Variation. *Trans. Glasg. geol. Soc.*, **19**, 390-403.
- . 1940. A Statistical Investigation of the *Anthracomys* of the Basal Similis-Pulchra Zone in Scotland. *Quart. J. geol. Soc. Lond.*, **96**, 13-37.
- . 1942. *Naiadites* from the Lower Carboniferous of Scotland; a Variation Study. *Trans. Glasg. geol. Soc.*, **20**, 208-221.
- . 1951. Biometrics and Systematics in relation to Palaeontology. In "A Joint Discussion with the Systematics Association, on Biometrics and Systematics. *Proc. Linn. Soc. Lond.*, **162**, 159-170.
- MCKERROW, W. S. 1952. Notes on the Species and Subspecies in Palaeontology. *Geol. Mag.*, **89**, 148-151.
- MACLENNAN, R. M. 1945. Generations in a Fossil Community. *Geol. Mag.*, **82**, 177-181.

- NOMURA, E. 1926 a. An Application of $a=kb^x$ in Expressing the Growth Relation in the Freshwater Bivalve *Sphaerium heterodon* Pils. *Sci. Rep. Tohoku Univ. (Biol.)*, 2, 57-62.
- . 1926 b. Further Studies on the Applicability of $a=kb^x$ in Expressing the Growth Relations in Molluscan Shells. *Sci. Rep. Tohoku Univ. (Biol.)*, 2, 63-84.
- SIMPSON, G. G. & ROE, A. 1939. *Quantitative Zoology*. New York and London.
- SYLVESTER-BRADLEY, P. C. 1951. The Subspecies in Palaeontology. *Geol. Mag.*, 88, 88-102.
- TRUEMAN, A. E. 1946. Stratigraphical Problems in the Coal Measures of Europe and North America. Anniversary Address of the President. *Quart. J. geol. Soc. Lond.*, 102, xlix-xciii.
- TRUEMAN, A. E. & WEIR, J. 1946-1952. A Monograph of British Carboniferous Non-Marine Lamellibranchia, Parts I (1946), II, III (1947), IV (1948), V (1951), VI (1952). *Palaeontogr. Soc.*

GROWTH AND PLANT SYSTEMATICS

By R. MELVILLE.

(With 4 text-figures.)

Plant taxonomists seem to have given little thought to growth processes as a factor likely to affect the soundness of the conclusions drawn from the plants they examine. Normally the taxonomist, working in the herbarium, examines the end products of growth, the mature leaves, flowers or fruits. The immature stages are of little use for his purpose, since they shrivel and become distorted on drying. Moreover, it frequently happens that the changes resulting in characters of critical or diagnostic value appear towards the end of the growth of an organ, or at least, they are not fully or characteristically developed in the immature structures. This tendency, observed in all plant organs, reaches its climax in the flowers and fruits, forming, as they do, the ultimate products of growth. The great emphasis placed on the reproductive structures in classical taxonomy derives further justification from physiological studies.

The physiologist is interested in growth as a dynamic process. He follows the changes taking place in an organism to their completion and in so doing is able to observe regularities that have escaped the notice of the classical taxonomist. Some physiological studies on growth have a direct bearing on taxonomic theory and others suggest lines of experimental research on taxonomic problems. This discussion will be confined mainly to such aspects, in which the physiological approach may be of assistance to the taxonomist.

It is sufficiently obvious that growth processes are important at all levels of organization within the plant down to the details of cytoplasmic structure. Microscopic details are the province of the cytologist and anatomist and rarely concern the taxonomist directly. It is sometimes necessary to fall back upon anatomical details in small plants such as *Lemna*, where some species are characterized by straight and others by sinuous walls to their epidermal cells. All start with straight walls, but different timing of the growth phases of the underlying tissues causes stresses that throw the walls into folds. The pith characters of *Juncus* spp. may be cited as a taxonomically valuable growth character at the tissue level. Here the cortical tissues expand to a greater extent than the pith, pulling out the pith into a delicate tracery of star-like cells with 12-14 arms. In different species the pith may be continuous and firm, or delicate, or finally ruptured to form septa at varying intervals along the stem.

The growth rhythms of species are relatively stable and result in the succession of leaf shapes and floral and other characters that enable us to assign numerous individuals to one species. The rhythm is modified and

morphological variation induced by the effects of environmental factors. Notable are changes in the length of day with their stimulation or retardation of flowering. A reduction in water supply and mineral deficiencies in the soil also tend to curtail the vegetative phase and lead to flowering. To some extent the plant is plastic under the onslaught of environmental conditions. The changes that take place are of such a nature that if continued they could lead to speciation. In general they may be classified into four groups :— (1) condensation by the reduction of internode length, resulting in the aggregation of similar or different organs ; (2) the reduction in the number of organs ; (3) fusion of similar or dissimilar organs ; (4) alterations in symmetry. Such morphological effects are the result of alterations in the timing and concentration of growth stimulants and possibly growth inhibitors. In spite of the great difference in appearance between a raceme and a capitulum, on physiological grounds one would expect the steps in the condensation sequence raceme $\rightarrow$ corymb $\rightarrow$ umbel $\rightarrow$ capitulum, to be fraught with no great difficulty. Each step may result from one or a few gene modifications and evolution along this line of development may have been rapid. Indeed, the early appearance of the Compositae would lend support to this idea. Whether the reduction or loss of the calyx in Umbelliferae and Compositae is necessarily correlated with the inflorescence changes, or is independently inherited, is at present unknown. Reduction in number may be correlated with an increase in size, as in *Camelina sativa*, in which Tedin (1925) has shown that a single gene is responsible for a reduction in the number of seeds per pod as well as their increase in size. This is explicable on a quantitative basis if the plants are producing similar amounts of reserve materials. Similarly I have observed that three species of Cedar, *Cedrus atlantica*, *C. libani* and *C. deodara* differ in leaf length and leaf number per fascicle in such a way that total leaf volume is approximately the same in all three.

The varying degrees in condensation of an inflorescence may be due to successive diminutions, in the production of a growth hormone controlling the elongation of the internodes until, finally, the hormone ceases to be produced. A similar process occurring in one of the floral whorls would lead to the reduction and ultimate loss of the whorl. Thus a condition of asepaly or apetaly may arise with comparatively small cytological changes.

The fusion of floral parts is probably the result of changes in the timing of the production of growth hormones in successive organs. If distinct pauses occur, the flowers are polysepalous and polypetalous. When there is overlap, the organ meristems become confluent. This may happen early in development and result in a tubular calyx or corolla or late and produce union at the base only. Similar alterations in the timing of the meristems of successive whorls would lead to epipetalous stamens, to perigyny and to epigyny. Probably the genetical control of all these processes is relatively simple. The concentration of growth hormones is involved, at least to the extent that below certain limiting concentrations, the meristems do not fuse.

Some years ago, D'Arcy Thompson (1942) pointed out that the change from polypetal to gamopetal can be represented by a series of Grandi's curves. The curves are plotted on polar coordinates and are represented by the general formula :

$$r = a + b \cos n\theta;$$

r , the radius vector, consists of two parts, a constant (a) and an expression representing the amplitude of the sine curve. For a pentamerous flower $n=5$. If we take the radius of the circle enclosing these figures (fig. 1) as unity then A has $a:b::9:1$, B has $a:b::3:1$ and when the petals are free, C , then a equals b and the formula reduces to :

$$r = \cos^2 \frac{5\theta}{2}.$$

Thus, with slight modifications of the constants, the curves slide easily into one another, just as in the plant polypetaly passes gently into increasing degrees of gamopetaly.

The growth processes here discussed are of profound importance to plant systematists, since they have been employed in the past to divide the dicotyledons into subclasses. Bentham and Hooker used these very distinctions for the definition of their subclasses Thalamiflorae, Calyciflorae, Gamopetalae and Monochlamydae. The artificial nature of their divisions has since been recognized on general grounds, but the probable simplicity of the underlying genetical changes has not apparently been recognized. The apparently rapid deployment of the Angiosperms, as a group, in the early stages of their evolution, which seems to be indicated by the scanty palaeobotanical evidence, is more readily understood if considerable morphological changes were the result of relatively simple genetical changes. The greater part of this evolution may have taken place in 2 or 3 million years. In looking back over the lapse of 150 million years or more, this would appear to us a rapid deployment.

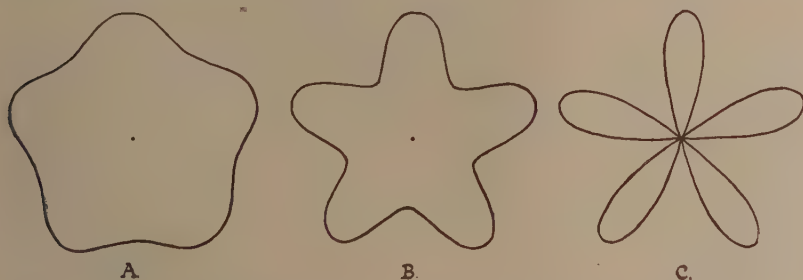


FIG. 1.—Grandi's curves representing two degrees of gamopetaly and polypetaly. Explanation in text. (After D'Arcy Thomson.)

The other class of growth change mentioned above, that of change in symmetry, is of high taxonomic significance. It is characteristic of many advanced taxa, such as the Labiateae and Orchidaceae, with their strongly zygomorphic flowers. The shapes of even comparatively simple asymmetric structures, such as an elm leaf, appear to depend upon the interplay of a group of genes. A considerable gene complex must be involved in controlling the shape of many zygomorphic flowers. Shape characters are therefore correlated group characters and as such are likely to be of greater taxonomic value than the simple characters of aggregation and reduction.

In recent years the problem of modifications of shape taking place during growth has received increasing attention from physiologists and to a lesser extent from systematists. Avery (1935) has demonstrated the presence of a decreasing auxin gradient from the base to the apex in tobacco (*Nicotiana*) leaves. This is correlated with a higher growth rate at the base than the apex. Delisle (1938) found that, in *Aster nova-angliae*, auxin concentration is at a maximum when cell division stops and elongation begins. The basal auricles on the leaves are late in forming and here the auxin concentration is maintained longer. In these examples the growth hormone concentration is linked with the shape changes in a similar manner. The absence, or degree of development of auricles, is a character taken note of by systematists.

A vast amount of study has been given to the phenomena of photoperiodism, but the field is too extensive to review here. It is evident, however, that growth hormones control the formative processes induced by alterations

in the light and temperature regimes to which plants are exposed. Leaf shape, habit and flowering time may be modified and the effects produced are similar to those distinguishing species or varieties under natural conditions. It seems highly probable that the development of the arborescent habit and delayed flowering among the tree *Senecios* and *Lobelias* of the East African mountains was a photoperiodic response subsequently fixed by natural selection. The passage from an annual habit among the beets, *Beta*, of the Eastern Mediterranean to the biennial or perennial condition in North West Europe is a similar phenomenon. Here there has been much discussion as to the limits of species and it seems that this group is still highly plastic to photoperiodic stimuli.

The successional changes in leaf shape, or in the degree of complexity of lobed or compound leaves, during the life of an annual plant, or in passing along the branch of a perennial, are extended or foreshortened by photoperiodic responses. There is, obviously, an interaction between the environmental responses and the inherited growth pattern characteristic of a species. In the past, this plasticity of leaf shape has led to its being regarded as of little critical value to systematists.

It is a matter of common observation, that the shape of the leaves on an annual plant changes in a regular manner, though successive leaves, from the first seedling leaf until the flowers are produced. When the leaves are lobed or compound, alterations in complexity accompany the changes in general shape. In perennial plants, comparable progressive modifications of leaf shape are observed on each annual growth increment of the shoot. These leaf shape phenomena have been attracting anew the attention of physiologists and Ashby (1948) has reviewed the field at some length in a recent essay on the morphogenesis of leaves. The correlation of the leaf shape changes with the age of the plant, or of the shoot on which they arise, has led to the conception of physiological age. The climax of these changes occurs at flowering time, after which there may be a partial regression towards the juvenile condition before growth ceases. The sort of change that takes place is well exemplified in cotton (*Gossypium*) (see Hutchinson, 1934; Hammond, 1941; Krenke, 1947). The earliest leaves are cordate and entire and successive leaves become more and more lobed and develop deeper sinuses, up to the flowering phase. Thereafter, reversion takes place and a simple cordate shape may again be reached. I have been referring to the leaf succession along the main stem, but if one examines the lateral branches it is apparent that partial reversion towards the juvenile condition occurs there also. In cotton the first leaf on a lateral branch may be like the one below that in the axil of which it arises, if on a lower branch, or there may be a difference of 2 or 3 leaves on the upper branches. These phenomena have led Krenke (1947) to formulate a theory of cyclic ageing and rejuvenescence in plants.

The cycle of leaf shape changes differs in different species. Again, taking cotton as an example, a comparison of the three species, *Gossypium herbaceum*, *G. hirsutum* and *G. barbadense*, as presented by Krenke (1947) is shown in fig. 2. There are evidently differences in timing and of the balance between the growth substances, that account for the differences between the species. Although individual leaves may resemble one another from species to species, the cycle of leaf shape changes as a whole may be quite distinctive. There is commonly sufficient difference to render this group character one of high taxonomic value. I have, in fact, been employing it successfully for some years in my treatment of the elms (*Ulmus*), where the flower and fruit characters are of little value.

From the taxonomic standpoint, the cycle of leaf shape changes may be treated as a single character. It is convenient to refer to it as a 'Leaf Spectrum'. As a complex character correlating a number of minor characters it may be

compared with the zygomorphic corolla, or with the correlated group of characters that are recognized in a *Ranunculus* flower. Separated, individual characters such as apocarp, polypetal, multiplicity of parts and achenial fruits are of little value alone. Correlated in a group, they acquire high taxonomic significance. It is the correlation of characters that matters and therein lies the significance of the leaf spectrum.

The leaf spectrum may prove to be of value even when the leaf shapes are very simple and I have recently used it in the description of two new species of *Epacris* (Melville, 1952). The drawings (fig. 3) were made from the leaves of one annual increment of individual representative shoots. They are in sequence, starting with the bud scales *a*, passing at *b*, to the foliage leaves of which only a few of the sequence are shown and exhibiting Krenke's so called rejuvenescence at the tip, *c-d*. If the lengths of the individual leaves

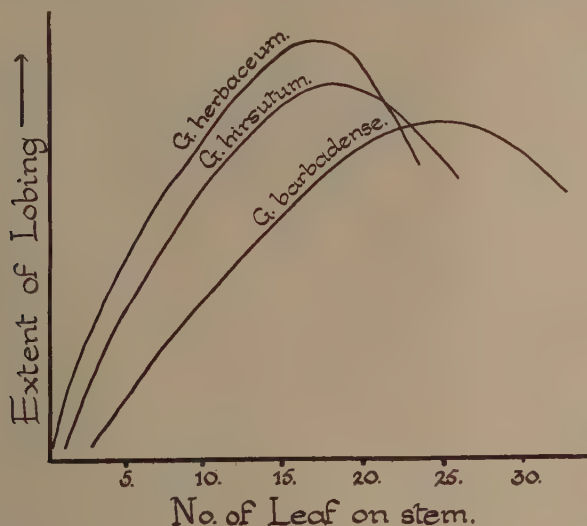


FIG. 2.—Differentiation between three species of cotton (*Gossypium*) in the extent of lobing of the leaves at successive positions on the stem. (After Krenke.)

are plotted against their breadths on a logarithmic scale, it is found that the points representing the leaves formed after the bud scales and before the final rejuvenescent phase of the cycle fall very nearly on a straight line (fig. 4). The straight line part of the graph includes the greater number of foliage leaves and the fact that it is straight, is an indication that the rates of growth, in length and in breadth, bear a constant ratio to one another, irrespective of the actual size reached by the individual leaves. When the straight line relationship holds, growth is said to be allometric and conforms with the allometry equation :

$$y = bx^k \text{ or expressed in its linear form :} \\ \text{Log } y = \text{Log } b + k \text{ Log } x.$$

Here *b* is a constant related to the initial difference between the length and breadth, when the phase of allometric growth starts and *k* is a constant representing the ratio between the growth rate in length to that of breadth. When *k* is unity the growth rates are equal and the graph rises at an angle of 45°; if *k* is greater than 1 (length plotted vertically) the graph rises more

steeply and growth in length is more rapid than growth in breadth. Similarly, if k is less than 1, the graph rises more gently and growth in breadth is more rapid than in length.

It is probable that an allometric growth relationship is maintained in many plants over part of the leaf spectrum. The measurements need not be confined to length and breadth, but measurements at various levels, or in various directions that may be of interest, or of the length of lobes or depths of sinuses, may be taken and combined in various ways. A set of growth data can be

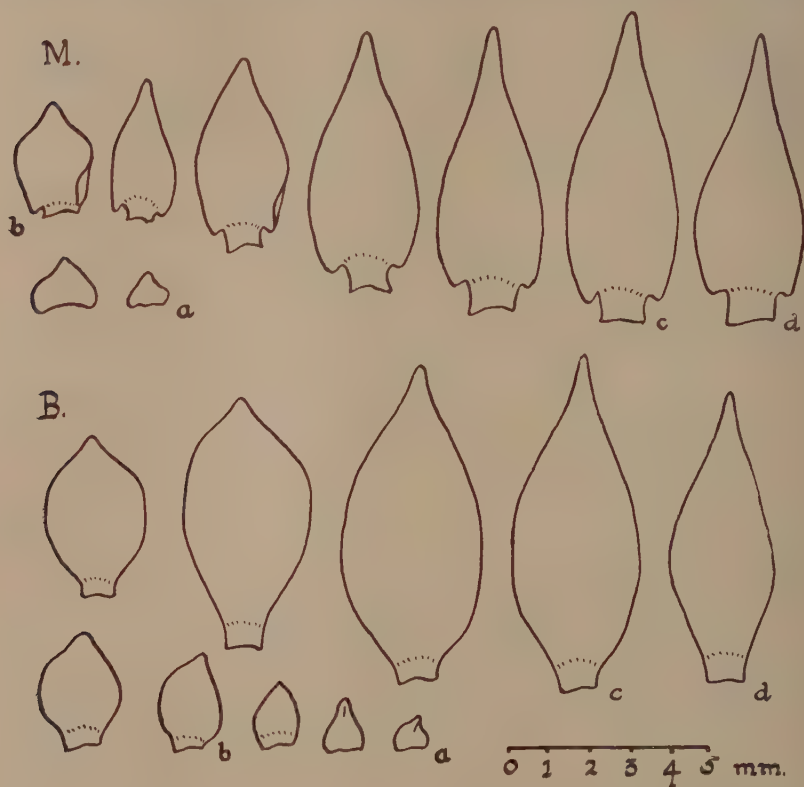


FIG. 3.—Leaf spectra of two species of *Epacris* showing the sequence of shape changes along the stem from bud scales, *a*, to foliage leaves, *b*–*d*, finishing with the so-called rejuvenescent phase of Krenke, *c*–*d*.

summarized in a concise and convenient manner in a graph and its slope is a character of value in the discrimination of species. Any series of similar organs on a plant, such as bracts or of sepals and petals in polypetalous forms, may form an allometric growth series.

The growth stages in the development of individual organs frequently form an allometric series, but as the taxonomist cannot measure them from his dried specimens they are of more interest to physiologists and experimental taxonomists. It would seem that allometric growth may take place during any phase of the growth cycle and that species or genera may differ in the stage at which this occurs. For example, Sinnott & Kaiser (1934) have demonstrated, that in various pure lines of the marrow, *Cucurbita pepo*, the

young ovaries already show the characteristic shapes that distinguish the ripe fruits, whereas in *Capsicum* the young ovaries are similar and differentiation in shape takes place after fertilization. In the marrow the allometric growth phase occurs very early, before the flower is half developed, and thereafter the relative growth rates, k , are near unity. In *Capsicum*, k is near unity before fertilization, but different strains are subsequently distinguished by different values of k .

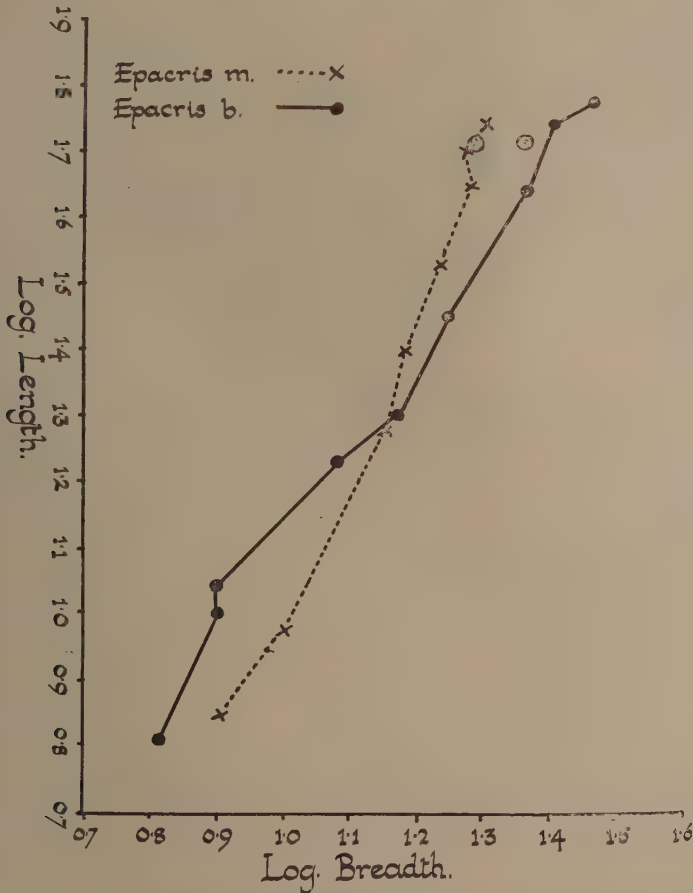


FIG. 4.—Logarithmic plottings of the lengths and breadths of successive leaves of two *Epacris* species, showing that even when a few leaves are taken from single shoots the growth relationships approximate to the requirements of the allometry equation. Circles mark the leaves of the so-called rejuvenescent phase of Krenke.

The allometric growth phase is not the only one of taxonomic interest in the leaf spectrum. Indeed, the beginning and ending of the spectrum may prove to be of greater discriminatory value. Thus, in *Epacris* the shapes of the bud scales may prove to be important, though I have not yet investigated this possibility. An examination of the leaf spectrum may throw light on

yet another kind of variation. Reverting again to *Epacris* (fig. 3 B), it was noticed that some plants of one of the species referred to earlier had much narrower leaves than the majority. Floral structure was similar and all appeared to be conspecific. In these plants the relatively senile narrow-leaved phase was reached earlier in the development of the shoot than in the majority of plants, although all were conforming to the general growth pattern of the species. It is possible that some environmental stimulus may have been the determining factor in deciding where in the leaf spectrum the mode of leaf shape shall occur. If this is the correct interpretation, it may provide an explanation for the existence of topoclines. Differentiation continued on similar lines would lead to speciation. Measurements of leaf spectra, or other correlated characters, may enable deductions to be made as to the trend and perhaps the order of evolution in a group, since the underlying changes take place in a circumscribed manner.

All the changes in shape observed along a leaf spectrum can be accounted for by differences in the balance between the growth factors responsible for the control of growth in different directions. During the allometric phase there is an approximately constant relationship between the factors controlling shape, but not size, with the result that the actual shape of a particular leaf depends upon its absolute size. Before and after the allometric phase the balance between all the growth factors is varying, though in a regular manner. The final phase in the sequence is not actually a reversion to a juvenile condition as suggested by Krenke's theory. Even in his example of the cottons, the final leaves, although simple in shape, have a different shape from those of the juvenile phase. Actually the comparison falls into error by over-simplification, brought about by the abstraction of too small a group of characters. In my example of *Epacris b.*, the final leaves do not in the least resemble those of the early phase. Considerable differences often exist between the leaf spectra of quite closely related species, even when some of the leaves nearly resemble one another. It is not difficult to accustom the eye to take in at a glance the whole gamut of leaf shapes. The leaf spectrum then becomes a group character of considerable taxonomic value.

Although it may be wrong to regard the final phase of the leaf spectrum as a reversion to a more juvenile condition, the change at the base of lateral shoots does appear to be of this nature. In many trees partial reversion occurs on shoots appearing after the removal of a limb and on the epicormic shoots developed from dormant buds on the trunk. Sucker shoots and coppice shoots often show a more or less complete reversion to the seedling phase of the species. The leaf succession on these shoots, taken together, exhibit a complete transition from the seedling to adult leaf shapes. The growth balance changes from year to year until the adult phase is reached. The route travelled in these changes and the growth balance at corresponding stages differ from one species to another. When suitable specimens are available they yield further data of taxonomic value, supplementary to that provided by the adult leaf spectra.

I have found leaf characters most useful in the study of the hybrid swarm which exists in the British elms. In *Ulmus* many species are interfertile and numerous segregates and back crosses occur, linking the species in a complex network. The value of the leaf characters depends upon differences in timing of the growth factors controlling leaf shape from one species to another. The final result is, that a shape occurring at one growth phase in one species is dominant in a hybrid, while, at other phases, characters from the other parent may be dominant. The dominance is not always complete and there is usually interaction between the shape characters of the two parents within the hybrid. One parent may be locally dominant in a particular shoot and the other in a neighbouring shoot, at the corresponding

growth phase. The difference in dominance here, may depend on environmental effects, acting in the early stages of leaf development, for the leaves do not develop simultaneously. Temperature and light intensity are possible controlling agents. Internal factors, such as local differences in the amounts of food reserves and other substances no doubt contribute to modify the balance between the effects of the two parents.

Time will not allow of the full development of this subject here and one example must suffice. An individual hybrid tree growing near Hitchin, Herts., was found with adult foliage resembling *Ulmus carpinifolia* so exactly in shape and size, that without other evidence it would readily pass for that species in the herbarium. The habit was intermediate between that of *U. carpinifolia* and *U. plotii* Druce, and the very dark green pigmentation of the leaves pointed to the latter species. On looking at the epicormic shoots, it was at once evident that *U. plotii* was involved, for the peculiar long shoots of that species, with characteristic leaf shapes, were there developed. Intermediate leaf shapes and others resembling those of *U. carpinifolia* were also found on the epicormic shoots. Thus, when the observer is familiar with the leaf shapes occurring in the various growth phases of the likely parents, it is possible to identify the parentage of a hybrid. The variability in leaf shape, which formerly was a stumbling block to botanists and caused them to place little value on leaf characters, has proved on critical study to be of high taxonomic importance, at least in this genus. There is no reason to believe that *Ulmus* is unique in this respect.

On looking back over the various aspects of growth discussed in this paper one is impressed by the stability of the growth mechanism of species. It is a dynamic stability, however, like that of a gyroscope, the balance of which can be changed to a new equilibrium by suitable forces. Appropriate forces appear to be supplied by the environment, but their effects are circumscribed by the existing genetical constitution and physiology of the plant. The previous history of a group determines the potential evolutionary trends of the future. The existing environment and natural selection do the guiding and sifting. The study of growth relationships may give us evidence of the paths taken and in the narrower field provide new methods and techniques for attacking our taxonomic problems.

BIBLIOGRAPHY.

- ASHBY, E. 1948. Studies in the Morphogenesis of leaves I. An essay on leaf shape. *New Phytol.*, **47**, 153.
- AVERY, G. S. 1935. Differential distribution of a phytohormone in the developing leaf of *Nicotiana*. *Bull. Torr. Bot. Cl.*, **62**, 313.
- DELISLE, A. L. 1938. Morphogenetical studies in the development of successive leaves in *Aster*. *Amer. J. Bot.*, **25**, 420.
- HAMMOND, D. 1941. The expression of genes for leaf shape in *Gossypium hirsutum* L. and *G. arboreum*. *Amer. J. Bot.*, **28**, 124.
- HUTCHINSON, J. B. 1934. The genetics of Cotton and the inheritance of leaf shape in Asiatic *Gossypiums*. *J. Genet.*, **28**, 437.
- KRENKE, N. 1947. See Summary of Krenke's work by E. Ashby in *Rep. Austral. N.Z. Ass. Adv. Sci.*, **1946**, 251-6.
- MELVILLE, R. 1952. Two allies of *Epacris heteronema* Lab. *Kew Bull.*, **2**, 175.
- SINNOTT, E. W. & KAISER, S. 1934. Two types of genetic control over the development of fruit shape. *Bull. Torr. Bot. Cl.*, **61**, 1.
- TEDIN, O. 1925. Vererbung, Variation und Systematik in der Gattung *Camelina*. *Hereditas*, **6**, 382.
- THOMSON, SIR D'ARCY W. 1942. *Growth and Form*, Ed. 2, 1046.

**PROCEEDINGS OF THE GENERAL MEETING HELD
3 April 1952**

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 20 March 1952, having been circulated, were taken as read, and confirmed.

The PRESIDENT read Messages received from the Private Secretaries of Her Majesty Queen Elizabeth, the Queen Mother, and Her Majesty Queen Mary, in reply to the Addresses of Condolence sent after the death of His Majesty King George VI, Patron of the Society.

Buckingham Palace,
22nd February, 1952.

Dear Sir,

I am commanded by Queen Elizabeth, The Queen Mother, to thank you and all those for whom you speak for your most kind message.

The thoughts and sympathy which surround her have greatly strengthened Her Majesty.

Yours faithfully,
O. DAWNAY,
Private Secretary.

The President,
The Linnean Society of London.

Marlborough House, S.W.1
18th February, 1952

Dear Sir,

I have had the honour of submitting to Queen Mary the humble address which you conveyed with your letter on behalf of the President, the Council and the Fellows of The Linnean Society of London, and I am commanded to express Her Majesty's sincere gratitude to all who joined in sending this touching message of sympathy in her great sorrow.

Yours very truly,
JOHN WICKHAM,
Private Secretary to
H.M. Queen Mary.

The Secretary,
The Linnean Society of London.

The following was thanked for a gift made to the Library since the last Meeting :—Miss M. H. Chambers.

The PRESIDENT reported the deaths of Miss Maud Williams, Fellow and Dr. Thomas Wayland Vaughan, Foreign Member.

Certificates of recommendation for election to Fellowship were read for the second time, in favour of the following candidates :—John Patrick Micklethwait Brenan, M.A., Miss Kathryn Benson-Evans, M.Sc., Francis Jessop Bingley, M.A., A. J. Boerman, M.D., Dr. Margaret Elizabeth Brown, M.A., Prof. C. G. C. Chesters, Douglas Graham Cowden, B.Sc., John Heslop Harrison, M.Sc., Ph.D., Thomas Raeside Laycock, B.Sc., Aleksandrs Melderis, Ph.D., Mahmoud Ahmed

Melouk, M.Sc., Ph.D., Francisco D'Ascensão Mendonça, Denys Morgan, B.Sc., S. K. Mukerjee, M.Sc., Ph.D., Mrs. Elsie H. Purnell, M.A., A. R. Ranjha, Prafulla Chandra Sharma, M.Sc., Mrs. Sybil Alice Stern, Kenneth Swinburne, Alasdair Ramsay Tainsch, M.B.E., B.A., Bernard Verdcourt, B.Sc., A.L.S., Owen Lynden Wade, M.A., M.D., M.R.C.P.(Lond.), A.L.S. and Derek Oliver Weitzel, B.Sc.

Certificates of recommendation for election to ordinary Associateship were read for the first time, in favour of the following candidates :—John Frederick Bradbury, Lewis Leonard Forman, B.Sc., Stuart Stanley Kidd, B.Sc. and Miss Joan Valerie van der Smagt.

The following were elected Auditors of the Treasurer's Accounts for 1951-52 under Chap. 10, Sect. 7 of the Bye-Laws :—

Representing the Council : Professor F. W. JANE,
Mr. H. R. HEWER.

Representing the Fellows : Mrs. VERA HIGGINS,
Dr. W. E. SWINTON.

The PRESIDENT announced that Mr. I. Henry Burkill, F.L.S., had been nominated to receive the Linnean Medal for 1952.

The following communications were read and discussed :—

Mr. P. R. BELL. Collecting Ferns in the Mountains of the New World Tropics (illustrated by coloured slides). (Discussed by the President, Mr. N. Y. Sandwith, Dr. J. Ramsbottom, O.B.E. and Dr. George Taylor ; Mr. Bell replied.)

Mr. FRANCIS ROSE. The Ecology of the Lowland Bog. (Discussed by the President and Dr. J. Ramsbottom, O.B.E. ; Mr. Rose replied.)

COLLECTING FERNS IN THE MOUNTAINS OF THE NEW WORLD TROPICS

By P. R. BELL.

In 1939 an expedition went from the University of Cambridge to the Blue Mountains of Jamaica. Although the outbreak of war interfered with its work, Dr. H. Hamshaw Thomas was able to collect and preserve for morphological work a large number of tropical ferns, among them a range of species of the genus *Elaphoglossum*. The relationships of this genus have long puzzled systematists and it was clear that no substantial advance could be made until its morphology was investigated. The investigation of the bulk of the Jamaican species has now been completed (Bell, 1950, 1951) and a number of morphological series have been demonstrated in the genus. It was realized that before conclusions of phylogeny or relationship could be made about the genus the study would have to be extended.

Elaphoglossum is a large genus of some 400 species (Tagawa, 1951), most of which grow in the rain forest of tropical mountains. The largest number of species occur in the Andes and there are far fewer species to be found in similar environments in the Old World. In 1951, with the aid of a grant from the Central Research Fund of the University of London and additional help from the University of Cambridge and the British Museum (Natural History), it was possible to arrange an expedition to the Ecuadorean Andes in order to

collect specimens of *Elaphoglossum* and other ferns for morphological and systematic studies. On the way to Ecuador, the opportunity was taken to visit the mountains of Jamaica and the Macarena Hills of Colombia.

In Jamaica several short expeditions were made to the mountains, including an ascent of Blue Mountain Peak. The richness of the Jamaican moss forest is, of course, well known, but the reading of descriptions beforehand cannot lessen the exhilaration a botanist experiences on seeing this wealth of cryptogamic vegetation for the first time. From Portland Gap at an altitude of about 4,500 ft. to the summit of Blue Mountain, an altitude of about 7,000 ft., the epiphytic vegetation was luxuriant and the filmy ferns growing by the side of the trail (such as *Hymenophyllum polyanthos*, *H. sericeum* and *H. lanatum*) were indicative of the constant high humidity in these forests. Several species of *Elaphoglossum* were encountered, including *E. latifolium*, *E. sellowianum* and *E. hirtum*, as well as *E. huacsaro*, a species not represented in the collections of the 1939 Expedition. The glades of tree ferns (of which *Cyathea pubescens*, *C. harrisii*, an endemic of Blue Mountain Peak, and *C. furfuracea* were the main components), although difficult to penetrate, proved a very rich introduction to the tropical fern flora. It was especially interesting to see representatives of the ancient ferns, such as *Marattia alata*, *Dicranopteris jamaicensis* and other members of the Gleicheniaceae, and the small epiphytic representatives of the advanced ferns, such as *Polypodium grisebachii* and *P. myosuroides*, some two inches or less in height. Unfortunately it was not possible to find on Blue Mountain Peak the interesting creeping species of *Elaphoglossum*, *E. nematorhizon*, described from there by Maxon.

Expeditions were also made to Cum See and Fox's Gap on the northern side of the Island and to Corn Puss Gap in the eastern part. As a result of these, material of *Elaphoglossum maxoni*, *E. crinitum*, *E. erinaceum* and *E. gramineum*, species not hitherto examined, was obtained for morphological investigation. It was an invaluable help to be accompanied in Jamaica by G. R. Proctor who was engaged in compiling a new ecological and systematic list of the ferns of the Island.

After this brief, but very valuable, visit to Jamaica, I flew across the Caribbean to Barranquilla and thence to Bogotá, Colombia. While in the capital, I received an unexpected invitation from the Colombian authorities through the British Council to visit the Macarena Hills in eastern part of the country. Dr. R. E. Schultes, the American explorer, and I went down to Villavicencio and from there flew out to the base camp by the side of the range. The first British botanist to explore the Macarena was Dr. W. R. Philipson in 1949 whose account has recently appeared (Philipson, Doncaster & Idrobo, 1951). As we had little time, we covered more or less the same ground as he had and ascended by his old trail to Pico Renjifo. *Elaphoglossum scalpellum* was collected on the Approach Ridge and *E. eximium* from the neighbourhood of the summit. We also made an extensive collection of bryophytes in this area. Unfortunately our activities were curtailed by the beginning of the rains, and where we ascended by dry paths, we returned through thick and slimy mud.

I flew on from Bogotá to Quito in Ecuador, arriving there as the rainy season of that region was finishing. I set up my headquarters in Quito, but the high Central Valley of Ecuador in which Quito is situated was not very rich for my purpose. It has been cultivated since earliest times and very little of the natural vegetation remains. The commonest trees, for example, are species of *Eucalyptus*, introduced from Australia about eighty years ago and now the main source of timber for building. There were few ferns to be seen, although *Pellaea ternifolia* was conspicuous on the mud walls about Quito. Almost all my collecting was done on the high ground and on the western and eastern slopes of the Andes down towards the steaming forests of the hot country.

One expedition included an ascent of Pichincha, the summit of which is about 15,000 ft. and just reaches the snow line. On the edge of the páramo there was a certain amount of cultivation, but there were numerous ferns along the loamy banks, amongst which were *Cystopteris fragilis*, *Elaphoglossum* spp., *Polystichum lehmannii*, *Adiantum wagneri*, *Botrychium virginianum* subsp. *meridionale* and, on the bushes, epiphytic species of *Polypodium*. Amongst the grass and bushes I observed with pleasure, as Spruce did nearly 100 years ago a little farther South (Spruce, 1908), that one of the commonest mosses of the páramo was *Pleurozium schreberi*. With increasing altitude the number of ferns diminished, and the grassy páramo vegetation became broken up by patches of bare gravel. At about 14,000 ft. the vegetation consisted of scattered tussocks of mosses and alpine. The striking *Lycopodium erythraeum* was frequently a component of these and in the shelter of a rocky ledge a small creeping species of *Elaphoglossum*, *E. ramosissimum*, was discovered. At the summit of the mountain *Polystichum polyphyllum* was found growing in a deep crevice amongst boulders.

One of the most productive expeditions to the hot country was that to the forest around the confluence of the Toachi and Pilatón rivers in the vicinity of Santo Domingo de los Colorados. This area has a very high rainfall and the collections were made in conditions that were far from pleasant and in country that was difficult to traverse. *Pityrogramma calomelanos*, *Trismeria trifoliata*, *Nephrolepis pendula*, *Anemia phyllitidis*, *Adiantum killipii* (which appears to be new to Ecuador) and *Elaphoglossum* spp. were among the ferns of rocky banks and *Hymenophyllum hirsutum*, *Trichomanes axillare*, *Vittaria remota*, *Antrophyum subsessile*, *Polytaenium lineatum* and *Elaphoglossum* spp. were among the epiphytes. The young red fronds of *Blechnum occidentale* were very conspicuous along the edges of trails.

Another very fruitful expedition was made to the district known as Pululagua to the N.W. of Quito. This is an extinct volcanic area that falls down in a series of steep valleys to the hot country around Nanegal. The collecting was done at an altitude of about 8,000 ft., the zone of the Andean bush forest, upon which, in this region, a thick fog descends in the afternoon and lasts well into the following morning. *Cheilanthes microphylla*, the very attractive *Pellaea rigida*, *Notholaena aurea*, *Polystichum platyphyllum*, *Anemia hirsuta*, *Adiantum patens*, *Dryopteris oligophylla*, *D. conformis* and *Asplenium monanthos* were some of the ferns on banks and by the sides of trails. The tropical form of the bracken also occurred here (*Pteridium arachnoideum*). Epiphytes were also abundant and included *Polypodium* spp., *Polytaenium lineatum* and *Elaphoglossum* spp. In several places by the sides of streams loamy banks were covered with *Anthoceros* spp. and *Elaphoglossum piloselloides*, a small tufted plant, the fertile fronds of which were conduplicate. The name "Pululagua" derives from two Indian words meaning "white cliffs" and probably refers to the outcrops of limestone that occur in this district. These limestone areas support a wealth of acrocarpic bryophytes, of which a representative collection was made.

The final expedition was made to the valley of the Pastaza, by which Spruce ascended from the Amazon to the Andean highlands. The first stop was at the little village of Puela and some very interesting collections were made on the northwestern slopes of Tungurahua, without, unfortunately, our seeing the summit of this famous volcano, which remained hidden in a heavy cap of cloud throughout our stay in the area. Besides the usual wealth of *Elaphoglossa*, there were numerous ferns, amongst which the curious *Blechnum sprucei*, which roots at the apex of the frond, was conspicuous. Later I descended to Baños and down the valley of the Pastaza as far as Rio Verde. There were many ferns to be collected here, too, including many more *Elaphoglossa*, the remarkable *E. trichophorum*, the fronds of which reach

almost a yard in length being especially noteworthy. *Hymenophyllum myriocarpum*, *H. polyanthos*, *Polypodium aureum*, *P. glaucum*, *Dryopteris patula* and several tree ferns were amongst the collections. Small thickets of *Equisetum giganteum* were met with several times in swampy places.

Together with these major expeditions, several smaller ones were made to the Cordilleras and páramos near Quito. Nearly 1,000 specimens were collected in Ecuador, of which 694 were Cryptogams. The morphological and systematic work upon them is now in progress. I have to thank especially Mr. A. H. G. Alston, whose extensive knowledge of the Pteridophyta has been at my disposal, and the generosity of the institutions named earlier.

LITERATURE.

- BELL, P. R. 1950. Studies in the Genus *Elaphoglossum* Schott. I. Stelar Structure in Relation to Habit. *Ann. Bot. N.S.*, **14**, 545-555.
 ———. 1951. Studies in the Genus *Elaphoglossum* Schott. II. The Root and Bud Traces. III. Anatomy of the Rhizome and Frond. *Ann. Bot. N.S.*, **15**, 333-346 and 347-377.
 PHILIPSON, W. R., DONCASTER, C. C., & IDROBO, J. M. 1951. An Expedition to the Sierra de la Macarena, Colombia. *Geog. J.*, **117**, 188-199.
 SPRUCE, R. 1908. *Notes of a Botanist on the Amazon and Andes*. London.
 TAGAWA, M. 1951. *Elaphoglossum* of Japan, Ryuku, and Formosa. *Mem. Coll. Sci. Kyoto (B)*, **20**, 26-31.

A SURVEY OF THE ECOLOGY OF THE BRITISH LOWLAND BOGS

By FRANCIS ROSE.

(With 8 text-figures.)

INTRODUCTION.

Although bog ecology in general is a topic that has fascinated botanists for many years, virtually no descriptive studies have so far appeared on the bog vegetation of the lowland British heaths. The only exceptions appear to be two papers by W. Watson, one by C. P. Petch (1945), and the account by Rankin of the Valley Moors of the New Forest in "Types of British Vegetation" by Tansley (1911). The first of these (1915) described the bryophyte zonation of a Somerset heath (Chard Common) which, however, appears from my own observations to be untypical of English wet heath and bog areas as a whole. The second (1932) gave full lists of species from several British moors and bogs, but did not attempt to describe the vegetation structure or plant associations. Petch's paper (1945) gave a very brief account of the vegetation of a boggy Norfolk heath. There has, of course, been much work on the upland blanket-bog and moor communities of Britain, and here the work of W. H. Pearsall is most outstanding: his paper (1941) on the Stainmore peat mosses is particularly interesting for comparison with the lowland areas. Much descriptive work, too, has been done, particularly by Swedish botanists, on the vegetation of raised bogs in areas of higher humidity than our eastern English lowlands; the most important British work of this kind is that of Godwin & Conway (1939), on Tregaron Bog in Wales, while in Sweden, Osvald (1923, 1948, 1950) and Du Rietz (1925, 1949, 1950 a, b, c) have carried out much of the classic work.

It was therefore felt that work was much needed to fill a big gap in our knowledge of the vegetation of lowland bogs in areas where rainfall is insufficient to cause ombrogenous bog development.

SCOPE OF THE WORK.

It was decided from the start that the work should be primarily a general survey of as many areas as possible, in order to get as full an idea of the range of variation in the vegetation of our lowland bogs, rather than a detailed study of one or a few areas which might later prove to be untypical or of merely local significance. It is hardly possible to select 'typical' areas until a large number and a wide variety have been examined in less detail. As the survey proceeded, it became possible to select certain areas for fuller examination. One hundred and twenty-two areas where bogs or remains of bogs occurred were examined.



FIG. 1.—Map of British Isles to show location of bogs studied.

These were distributed over the lowland parts of Britain as follows (fig. 1):—

- 34 sites on the Folkestone Sands of Kent, Sussex, Surrey and Hampshire.
- 3 sites on the Hythe Beds of Surrey and Sussex.
- 14 sites on the Hastings Sands of the Weald of Kent and Sussex.
- 18 sites on the Bagshot and other Upper Tertiary sands of the London Basin.

- 12 sites on the Glacial Sands of East Anglia and Lincolnshire.
- 4 sites on the Lower Greensand of W. Norfolk.
- 12 sites on the Upper Tertiary sands of the New Forest and East Dorset.
- 3 sites on the Lower London Tertiaries.
- 4 sites on the glacial gravels of the London Basin.
- 1 site on the old red sandstone of E. Somerset.
- 11 areas of more or less modified raised and flat bog in the Midlands and Northern England.
- 6 lowland bog areas in Scotland, in Strathspey and West Inverness, for comparison with the above.

The work was thus primarily a survey of as much as possible of the existing lowland 'valley-bog' vegetation of east and south England, with bog areas in other parts of Britain brought in for comparison. A little work was done in places on the stratigraphy to try to get information on the way in which the bogs had developed.

CLASSIFICATION OF BOG TYPES STUDIED.

With the exception of the remnants of raised bog mentioned above, the great majority of the bogs studied proved to be of the 'valley-bog' type of Tansley (1939), in which the wetness of the habitat is maintained largely by mineral ground water either flowing into the bog from above or from seepage zones at the sides. Such 'soligenous' bogs are classified as 'poor fen' by Swedish ecologists (Du Rietz, 1949, 1950 c), who regard any peat mire, whether alkaline, neutral or acid, as a fen if the water supply is primarily derived from the surrounding ground. This classification, although strange to British ecologists, is useful in considering our lowland valley-bogs, as every variation can be found in them from the highly acid to the highly alkaline.

STRUCTURE OF LOWLAND BRITISH VALLEY-BOGS AND COMPARISON WITH RAISED BOGS.

In the actual plant-communities present, the lowland valley-bogs of Britain show a great similarity to typical raised bogs and their associated marginal fens or 'laggs', but the arrangement, sequence in space, and sequence in time of the communities is very different. In raised bog, a central area of sphagnum-dominated vegetation (compare the 'moss-heath' of Conway (1949)) develops over a former fen which has in turn invaded an aquatic or swamp community. Fen communities persist round the margins of this central raised area where mineral soil-water influence is felt most strongly, and these tend to show a zonation, the most base-rich types of fen being usually furthest from the raised central *Sphagnum* area. In between these 'lagg' areas and the sphagnum bog proper there is usually a slope or 'rand' with better drainage and consequently a vegetation more of the heathland type, often with pine trees. In valley-bog, the fen communities occupy a central position where conditions are wettest, and, owing to the greater volume of drainage water, soluble salts are in best supply. The sphagnum bog zone lies marginally to this and derives its water supply from the drainage seeping in from the extremely base-poor sands or gravels which always occur on the valley sides where bogs of this type are formed. Outside the sphagnum-hummock zone (which is very like the hummock-and-hollow complex of raised bog) there are usually readily distinguishable communities in two or three zones in progressively drier habitats, and finally dry heathland over a podsol (fig. 2).

ZONATION.

The detailed zonation of typical valley-bog is described below. Owing to variations in topography, one or more of the zones may be absent, or even duplicated.

Starting from the centre we have the following zones :—

1. Carr or swamp-carr along the central stream, if this is present, as is usually the case in the larger bogs with median drainage.
2. Poor fen or reed swamp, with little or no *Sphagnum*.
3. *Sphagnum pulchrum*-*Eriophorum angustifolium*-*Juncus sylvaticus*-*Molinia* association.
4. *Sphagnum* hummock complex.
5. Wet-heath.
6. Damp-heath over a definite peat layer.
7. Dry heath over a thinner peat layer.
8. The surrounding dry heath or bracken communities with little or no peat, a typical podsol soil profile, and a deep water table.

The vegetation of these zones will now be considered in turn.

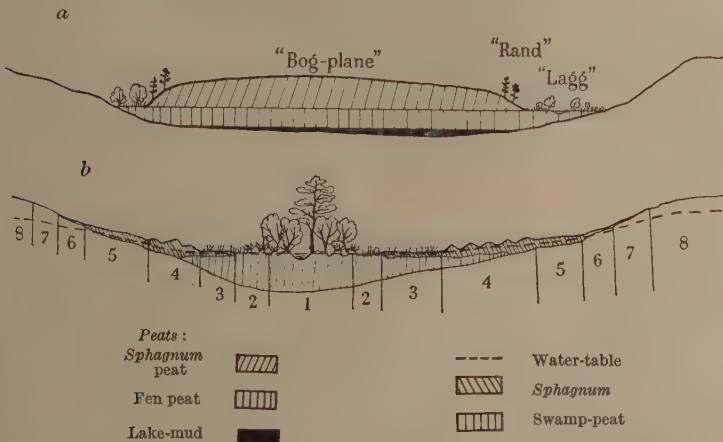


FIG. 2.—Diagrammatic cross-sections of raised-bog (a) and valley-bog (b), with zonation of the latter shown.

1. The Carr.

This community is dominated as a rule by *Salix atrocinerea*, sometimes with an innermost zone of *Alnus glutinosa*. It is determined by the constantly high watertable, which is usually at or even above the soil surface, by the continuous flushing by whatever mineral salts there are available in the total water supply of the bog, and by the better oxygenation associated with the moving water as compared with the more stagnant conditions on either side. In small bogs it may be absent. The field layer may contain a variety of fen carr species, especially *Carex paniculata* and *Carex canescens*.

2. The Swamp or Poor Fen Zone.

This represents a zone rather similar to 1 in habitat factors, but being removed from the stream, conditions are more stagnant and tree growth less

vigorous. The tendency to winter flooding may check any rapid spread of *Sphagnum* communities into it, but often this zone appears to be seral, and in process of invasion by bushes of *Salix* or carpets of *Sphagnum*.

The vegetation shows a variety of dominants depending on the base status. In valleys with relatively base-rich water, the swamp-carr field layer of *Carex paniculata* tussocks may extend into it, or the swamp of *Equisetum limosum* may occur. In poorer waters, *Carex rostrata*, *Menyanthes* or *Juncus sylvaticus* may be dominant or abundant. *Sphagna* of low acidity, such as *S. squarrosum*, *S. recurvum*, *S. fimbriatum*, and *S. palustre*, may occur as local communities in this and the previous zone. These species are all shade-tolerant, unlike the *Sphagna* of Zone 4.

3. *Sphagnum pulchrum*–*Eriophorum*–*Juncus* Association.

This community usually takes the form of a carpet over liquid peat which, like 1 and 2 will not bear the weight of a man—in fact, the ‘peat’ is more like a soup in consistency than a real peat. Apparently it is formed by the colonization of a zone like 2 by loose golden carpets of *Sphagnum pulchrum*, often preceded by *Polytrichum commune*. The zone is subject to seasonal water level changes, and is often of a floating character, but is evidently sufficiently stagnant and stabilized to enable the *Sphagnum* to spread from the margins. The acidity produced by the *Sphagnum* carpet results in a more acidic type of vegetation of higher plants. Other *Sphagna*, such as *S. palustre* and *S. recurvum*, may occur in this zone, and species such as *Hypericum elodes*, *Carex demissa*, *Myosotis secunda*, *Scutellaria minor*, and *Narthecium*. When the zone is rather drier, a *Molinia*-hummock system may develop, and the *Sphagna* may grow over this to initiate a hummock complex as at Hurston Warren in West Sussex. Conditions beneath the surface of Zone 3 are always highly reducing, except in extreme droughts.

4. The *Sphagnum* Hummock Complex.

This zone is the one which, in the actual plant communities present, bears the greatest resemblance to the vegetation of an active raised bog surface.

Sphagna form the most prominent part of the vegetation, and by their growth a hummock and hollow complex is developed. An actual complete cycle can in some cases be demonstrated, as at Thursley Common, but more often the bog is too young to show more than a simple succession from a Zone 3 type of community to a raised hummock crowned with *Calluna* and *Erica tetralix*. The pool-hollows are dominated by the aquatic *S. cuspidatum*, which is invaded in places by carpets of *S. pulchrum*, or else directly by the main hummock former *S. papillosum*. *S. papillosum* hummocks may also develop over *S. pulchrum* carpets. Next the tops of the hummocks develop caps of the crimson *S. rubellum*, or, in certain bogs, the fat pinky-red *S. magellanicum*, which tends to take over locally the rôle of both *S. papillosum* and *S. rubellum* in those valley-bogs (twelve such observed in S.E. England) where it occurs. Finally lichen degeneration of the hummocks may occur.

Species which may be associated with the *Sphagna* in each of these phases are :—

S. cuspidatum phase :—*Rhynchospora alba*, *Eriophorum angustifolium*, *Drosera anglica* (very local, New Forest and Norfolk Broads only), *Drosera intermedia*, *Juncus bulbosus*, *Drepanocladus fluitans*, *D. revoluens*, *Campyllum stellatum*, *Scorpidium scorpioides*, *Cephalozia fluitans*, *C. francisci*. *Sphagnum subsecundum* in one or other of its robust, highly coloured forms may replace *S. cuspidatum*.

S. pulchrum phase :—*Narthecium ossifragum*, *Eriophorum angustifolium*, *Drosera rotundifolia*, *Acrocladium stramineum*.

S. papillosum phase:—*Narthecium*, *Eriophorum angustifolium*, *Erica tetralix*, *Molinia* (very frequent, but weak and non-tussock forming), *Drosera rotundifolia*, *Oxycoccus quadripetala* (in some of the larger bogs only); *Polytrichum commune* as an alternative hummock former, which may in turn be smothered by *S. papillosum*; and a number of hepatics. *Odontoschisma sphagni* and *Leptoscyphus anomalus* are both very constant hepatics which carpet the *Sphagnum* and check its growth locally, or else grow in small patches up the sides of the hummocks. *Cephalozia macrostachya* is usually prominent in small hollows, and is a characteristic and nearly constant species of this phase (21 localities observed).

S. rubellum phase:—*Calluna* (entering for the first time), *Erica tetralix*, *Drosera rotundifolia*, *Oxycoccus* (where it occurs it may become dominant in a tangled carpet over the hummocks), *Eriophorum vaginatum* (rare), *Aulacomnium palustre*, *Polytrichum strictum*, and a still richer hepatic flora—the delicate *Lepidozia setacea*, various species of *Cephalozia*, especially *C. macrostachya* and *C. connivens*, *Aneura latifrons*, *Calypogeia trichomanis*, and *Calypogeia sphagnicola* (rare), besides those previously mentioned. Blue green algae occur, and a species of the small agaricaceous fungus *Galera*. Lichen colonization of the drying hummock tops under the *Calluna* is by such species as *Cladonia sylvatica*, *C. furcata*, *C. uncialis*, etc. An interesting phase of hummock-degeneration can be observed in about six of the larger bogs. Here the *Sphagnum rubellum* becomes overgrown by carpets of the large entire leaved hepatics *Leptoscyphus anomalus* and *Odontoschisma sphagni*, which require the well drained, highly acid environment such as the firm *S. rubellum* hummocks provide. This results in a growth check of the affected part of the hummock. Meanwhile the surrounding unaffected *Sphagnum* 'turf' continues growth, so that what was a hummock or at least part of an elevated level carpet becomes a hollow. The greater wetness enables growth of *Cephalozia macrostachya* to replace the two above hepatics, sometimes with a little *Aneura latifrons*. Eventually, the rising surface of the *Sphagnum* carpet relative to the new hollow results in this hollow being submerged, either by an absolute rise of water-table, or more often through the sinking of the whole surface *Sphagnum* carpet by its increasing weight, since the underlying peat is usually still uncompressed and soup-like. Then the aquatic bog pool species *Cephalozia fluitans* and *C. francisci* supervene, in turn to be overwhelmed by the development of a new *Sphagnum cuspidatum* carpet. These stages can be demonstrated by simple surface borings, just as can the stages of hummock development. A similar phenomenon has been noted by Osvald (1950) at the raised bog Komosse in Sweden.

It will be noted that this hummock-association is practically identical with the active raised bog hummock complex in vegetation, but apart from lacking certain species prominent in most W. European raised bogs (*Andromeda polifolia*, *Empetrum nigrum*, *Vaccinium vitis-idaea*), and showing only very rarely a large development of *Eriophorum vaginatum* and *Trichophorum caespitosum*, so characteristic of most raised bogs, it differs in that it is usually a relatively recent development either over very shallow heath land peat, or over previous poor-fen or acid swamp community, and not a long standing community of great age over deep, compacted peat.

5. The Wet-heath Zone.

This zone is almost invariably to be met with immediately above Zone 4. It is essentially a heath community, dominated either by *Erica tetralix* or more usually by varying amounts of this with *Calluna*. The community can usually be distinguished readily by the eye in the field, though to determine its exact composition statistical analysis is necessary. Methods involving the counting

of shoots show that two wet-heath communities visually-dominated by *Calluna* or *Erica tetralix* respectively, may give similar numbers of shoots of each species. Thus to get a true estimate of the actual development of each species, 'cropping' methods involving harvesting all the shoots of each species and obtaining the dry weight of each would be necessary. This has not been attempted in the course of the present work, as it was not felt necessary for the recognition of what is a community, well marked in its habitat, structure, and associated species. The wet-heath zone is definable as the zone of the valley-bog complex which shows, beneath its *Calluna-Erica tetralix* 'shrub-layer', a more or less continuous carpet of the two *Sphagna*, *S. tenellum* and *S. compactum*. *S. tenellum* may occur in parallel situations to *S. rubellum* on the bog hummocks of Zone 4, but only rarely, while *S. compactum* is confined, in the writer's experience, to this zone. The community is developed over a shallow layer of firm structureless peat (both the *Sphagna* concerned are poor peat formers), where the winter water table is near the surface or temporarily above, and, where in summer it is normally not more than 6 inches down, except in droughts. The soil, which shows typical gley features, is usually saturated most of the year.

This zone is that in which *Eriophorum vaginatum* (met with in nine areas) and *Scirpus caespitosus* (about twenty areas) usually occur in S.E. England. Their presence here rather than in Zone 4 may be correlated with the firmer substratum and better drainage, more like the conditions of old raised bog. The two sundews, *Drosera rotundifolia* and (especially) *D. longifolia*, are very plentiful in most places in this zone, and locally, where patches of bare peat occur, covered only with the purple alga *Zygogonium ericetorum*, *Lycopodium inundatum* may be found in more or less abundance (nine areas). Other species include: *Molinia coerulea* (usually plentiful but weak except after fires, when it may become dominant), *Narhegium ossifragum*, *Dicranum bonjeani*, and carpets of the small hepatic *Gymnocolea inflata*. The lower margin of this zone merges into Zone 4 and sometimes, if the gradient is not too steep, there is a tendency for Zone 4 to invade Zone 5 slightly. Generally, however, the zones are fairly stable. In some valleys or shallow depressions on heaths, Zone 5 may be the lowest present when the permanent water table nowhere reaches the surface of the mineral ground.

6. Damp-heath.

This zone occurs on gentle gradients above Zone 5. It is dominated by *Calluna* with more or less abundance of *Erica tetralix* and *Molinia*, and is characterized by a lower water table than 5. Only in very wet weather does water temporarily lie on the surface, and normally the ground is merely damp. A thin layer of peat overlies a more or less typical podsol, which is usually somewhat gleyed above. The peat is formed partly from the dwarf shrubs and partly from *Molinia* (which, as in 5, may become quite dominant after repeated fires), and also from bryophytes, algae and lichens.

The most characteristic bryophytes of this zone, species which are almost confined to it in S.E. England, are the mosses *Campylopus brevipilus* (18 sites), *Dicranum spurium* (15 sites) and *Hypnum imponens* (rarer, 7 sites only). They occur usually in a narrow intermittent belt, and vary from subdominance and more or less universal distribution in some Zone 6 areas to occurrence as odd scattered tufts elsewhere. Lichens, especially species of *Cladonia* (*C. coccifera*, *C. pyxidata*, *C. sylvatica*, *C. uncialis*, *C. furcata*, *C. rangiformis*) together with the hepatic *Gymnocolea inflata* and the usual dry heath mosses (*Pleurozium schreberi*, *Dicranum scoparium*, *Hypnum cupressiforme* var. *ericetorum*). In bared areas in Zones 5 and 6 the primary visible colonist of the damp sand is usually *Zygogonium ericetorum*.

7. Dry Heath with Peat Layer.

In this zone the water table is usually far below the surface, and the zone has all the characteristics of typical dry *Calluna* heath with a well-developed moss and lichen layer. Very often there is an abrupt change from Zone 5 (or even 4) to Zone 7 where an impervious bed throws out water as a seepage zone on a steep slope.

8. Dry Heath Communities with no Peat Development.

These may occur above Zone 7 in the driest areas of the heath, but the absence of peat may be due to repeated fires which have failed to burn the wetter peat of lower zones. Often *Pteridium* invades such areas heavily; the improved soil aeration associated with absence of a peat layer may aid the bracken.

VARIATIONS IN THE GENERAL PATTERN—LOCAL TYPES OF VALLEY-BOGS.

The structure and zonation so far described is that of the typical larger bogs. These are developed usually in heathland areas on sand or gravel subsoils, where valleys cut down through the highly pervious strata to either local seams or deeper beds of impervious clay.

Where the loamy Sandgate Beds underlie the sandy Folkestone Beds, or Barton Beds underlie Bagshot Sand, such bogs may form where valleys cut down to the impervious lower strata. Springs or flushes will occur along the margins and at the head of the valley and a swamp will develop, and later on the establishment of the typical zonation will supervene. Sometimes a perched water table on the valley sides produces lateral terraces of Zones 4 and 5 separated from the valley floor bog (e.g. Ambersham, Heyshott, Chobham, Caesar's Camp. As before mentioned, if the valley is not deep enough, or is too small to possess a permanent flow of water, one or more of the lower zones may be absent. At Matley and Wilverley Bogs, New Forest; Short-heath, N.E. Hants; Bog Common and Hurston Warren, West Sussex; Chobham Common, N.W. Surrey; and Hothfield Common, E. Kent, the full zonation can be seen. At Heyshott and Ambersham Commons, W. Sussex; Caesar's Camp, S.E. Berks; and at Thursley Common in Surrey, the two lowest zones are missing, a hummock-complex of Zone 4 type occupying the centre of the bogs; while at Trotton and Iping Commons, W. Sussex; Oakhanger, N.E. Hants; Chailey, E. Sussex; and in much of Ashdown Forest, the lowest zone present is 5. Hence the species confined to the lower zones will be absent from such valleys, though traces of development of lower zones may be visible at the lowest parts of the valleys. Apart from these variations in the physical structure of valley-bogs, chemical variations in the nature of the water supply occur, particularly in E. Anglia. On some of the West Norfolk Greensand areas (Roydon Common, Blackborough, Derby, Sugar and Dersingham Fens) outliers of chalky boulder clay or calcareous marl of glacial origin may occur in pockets or hollows on the Greensand. In East Norfolk (e.g. Buxton Heath, Bryant's Heath, Redgrave Fen) valleys have cut down through glacial sands and gravels to older Chalky Boulder Clay beneath. In both these areas, the result is a valley which has acidic soil conditions on the upper slopes, and highly calcareous ones in the bottom. Here the upper zones down to 4 tend to be much as usual, Zone 4 occurring where the base-poor (oligotrophic) drainage water from the sands or gravels meets the surface on the sides of the valley as a marginal flush. The lower zones, may, however, be replaced by various rich-fen communities. If the oligotrophic water table of the sands is a perched one, as happens at Buxton Heath, a zone of slightly damp (in September) calcareous meadow may occur below this where, as here, there is some grazing, and then below that, where the

calcareous water table in turn reaches the surface, mixed fen will occur. The central stream is bordered, if in its apparently natural condition, with typical fen-carr of East Anglian type. Thus a very great range of plant communities and species may occur in a small area.

At Buxton Heath, where this is better observed, apparently, than anywhere else, the calcareous meadow zone contains the following species: *Molinia caerulea* d, *Anthoxanthum odoratum* va, *Agrostis canina* va, *Seiglingia decumbens* va, *Juncus subnodulosus* a, *Potentilla erecta* va, *Succisa pratensis* a, *Centaurea nigra* a, *Briza media* va, *Trifolium pratense* f, *Erica tetralix* f, *Galium uliginosum* etc. showing a mixture of 'calcicole' and 'calcifuge' species. Peat was c. 10 cm. deep, and moist, and underlain by marly sand.

The mixed fen (pH 7.4) contained such species as *Juncus subnodulosus* d, *Epipactis palustris*, *Schoenus nigricans*, *Parnassia*, *Drosera anglica*, hummocks of *Sphagnum squarrosum* (pH 6.3) and *S. plumulosum* (pH 6.1), and a very rich flora of calcicolous fen bryophytes forming a dense carpet. This included *Philonotis calcarea*, *Drepanocladus vernicosus*, *Cratoneuron falcatum*, *Acrocladium giganteum* and *cuspidatum*, *Mnium affine* (and *Lophozia schultzei*, which, though only known in Britain hitherto in one fen in Norfolk, was found to be abundant here).

A smaller type of soligenous bog occurs on some heathlands where the ground is much dissected. This is the 'spring' or 'flush' bog, and consists of a (usually small) area of Zone 4 community, often margined laterally by the other upper zones, on a steep slope where the water-table reaches the surface. It is essentially a fragment of the typical valley-bog, differing only in detail in its often better oxygenation and drainage, though even this is not always true. Sometimes a small area of poor-fen community occurs at its drainage outlet. Such bogs are the main type in Ashdown Forest where seams of clay or harder sandstone often throw out springs well above the floors of the older valleys.

At Thursley in Surrey there occurs a fairly large bog (about 5 acres) which is essentially soligenous in type in that it shows no general rise in level above the mineral soil water-table of the depression in which it lies, but which nevertheless shows an approach to the raised bog type in general structure. At the very gently sloping margins on the mineral ground, the usual Zones 5, 6 and 7 are to be found, though the transition between 6 and 7 is indefinite owing to the nearly level ground. The whole central area of the bog, however, consists of a large level expanse of Zone 4 type, mostly dominated by *Sphagnum papillosum* (70 per cent) with also *Sphagnum pulchrum* (about 19 per cent), *Sphagnum tenellum* (8 per cent) forming a fairly even carpet, and scattered hummocks of *S. rubellum* and *S. magellanicum*, also with scattered *S. cuspidatum*-dominated pools. Borings indicated that this bog commenced as a shallow pool of open water (indicated by a layer of blue-black peaty mud), later invaded by *Eriophorum angustifolium* swamp, and finally by *Sphagnum*, in some cases *S. cuspidatum*, but mostly by the species now dominating the surface. With its abundance locally of *Oxycoccus*, *Polytrichum strictum* and *Calluna* on the hummocks among *Erica tetralix*, and its high acidity (pH 4.9 in the pools, 3.9 in the hummocks of *S. rubellum*, 4.1 in the *S. papillosum* carpet), the resemblance to active raised bog such as considered below is indeed striking. The depth of this bog to the mineral soil is only 110 cm. in the deepest parts, so it must be fairly young, and in view of the rainfall of this part of Surrey (just under 30 inches per annum), it may yet develop into an ombrogenous bog. Indeed, many of the *Sphagnum rubellum* hummocks already rise 1 foot 6 inches (c. 47 cm.) above the water table, and they are still growing. There is a close parallel between this flat type of *Sphagnum* bog and the type described from Minnesota by Conway (1949).

In the N.W. Midlands, in Cheshire, Staffordshire and Shropshire, there

occur bogs of essentially similar type though of much greater age than that at Thursley. Wybunbury Moss in Cheshire is one of the best examples extant of this sort. Here a hollow in the boulder clay dammed by a glacial moraine has developed into a lake, which is now occupied by a virtually flat *Sphagnum* bog with very similar surface vegetation to that at Thursley. At Wybunbury however the flora is far closer to that of typical northern English raised bog, and *Andromeda*, *Oxycoccus*, *Empetrum*, and *Eriophorum vaginatum* are abundant (the last two often being dominant on drier hummocks), locally, *Vaccinium vitis-idaea* occurs where birch or pine has formed woodland over the *Sphagnum*. *Andromeda*, *Empetrum*, and *Vaccinium vitis-idaea* are not known in *Sphagneta* in the south-eastern valley-bogs, though *Empetrum* formerly occurred in the long derelict raised bog at Amberley in Sussex, and *Andromeda* was formerly recorded at Larlingford near Thetford in Norfolk. The aspect of the surface of the open *Sphagnetum* at Wybunbury Moss is intermediate in character between that of a typical south-eastern 'Zone 4' and that of the 'regeneration complex' of a typical raised bog, such as Tregaron Bog in Wales, Corpach Moss near Fort William (Inverness-shire), or Austwick Moss in Yorkshire. The large proportion of the open surface occupied by very wet carpets of *Sphagnum pulchrum* with *Eriophorum angustifolium* indicates the essentially soligenous character of Wybunbury Moss. A small lakelet with open water exists on the bog, invaded by *Eriophorum angustifolium* and *Sphagnum cuspidatum*. This appears to represent a relic of the former open lake. I have made no borings here, but Mr. M. D. Poore, who has carried out a series of borings, informs me that the apparently deep and solid *Sphagnum* peat of the Moss is underlaid by water several feet deep. I am much indebted to him for this information. The bog is therefore of the floating raft type of lake-bog essentially similar to that at Thursley and the Louisa lake bog described below.

Chartley Moss in Staffordshire is essentially similar in flora and structure to Wybunbury Moss, and shows similar lakelets, though here there are three of them. Chartley Moss, however, has been partly drained, and in the ditches of the drained eastern part the peat can be seen in section. Several feet of compact solid peat are visible here, and give some evidence of possible ombrogenous development, but extensive borings are needed here to elucidate the true history of the bog.

Several stages in the development of bogs of the Wybunbury type can be seen bordering some of the Cheshire and Shropshire meres, but this is perhaps not the place to discuss these north-west midland lake-bogs in detail. They are a study by themselves.

The former presence at Wybunbury and Bomere (Shropshire) of *Scheuchzeria palustris*, a species characteristic of large wet bog pools and oligotrophic lakes in north-west and central Europe, is noteworthy. This plant formerly occurred widely in raised- and lake-bogs in Britain as we know from specimens and remains found in peat-stratigraphical work (Hardy, 1939; Clapham & Godwin, 1943), and was at Wybunbury until as late as 1895. It is now apparently extinct, however, except on Rannoch Moor, a Scottish blanket-bog area (Sledge, 1949). There is as yet no evidence that this species has ever occurred in the S.E. English soligenous bogs, although there exist at present many apparently suitable habitats. Most of these bogs, however, appear to be of relatively recent origin, to judge from their shallow peat deposits, and *Scheuchzeria*, a species most at home in cold climates, may well have receded northwards before their development occurred. Nevertheless, it is known to have occurred as near as the former raised bogs of Shapwick, Somerset.

REGIONAL FLORISTIC VARIATIONS.

Even within the relatively small area of Britain (from Lincoln to Dorset) in which well developed lowland valley-bogs occur, there are interesting

variations in species content in the plant associations. These seem inexplicable on ecological grounds, and still more inexplicable on grounds of general geographical distribution, as the total extent of country and climatic range involved is so small.

One of these variations is to be seen in the absence at the present day from all the bogs of East Anglia, including Essex, of *Narthecium ossifragum*, with the sole exception of the small area of the Greensand in West Norfolk. There are a few old records for East Norfolk, but, although suitable habitats remain, the species cannot now be found. Still more remarkable is the apparent entire absence of *Oxycoccus* from all bogs developed over the Upper Tertiary sandy strata in S.E. England, both in the New Forest–East Dorset region and the Bagshot area proper in N.W. Surrey, N.E. Hants and S.E. Berks. The species, it is true, is very rare generally in S.E. England ; but it still occurs in abundance in bogs over the Folkestone Sands (Upper Cretaceous) in three localities, one each in N. Hants, S.W. Surrey and West Sussex. Formerly, too, it apparently had several other stations in bogs now modified or destroyed on both the Greensand and the Ashdown Sands of Sussex and Surrey. There appear to be many more suitable habitats for this plant in the New Forest but there is no evidence yet that it has ever occurred there. It is improbable that the cause is some nutritional deficiency in water draining from the Tertiary Sands, since elsewhere *Oxycoccus* is most typical of true ombrogenous bog with virtually no supply of minerals in solution at all from the soil water.

On the other hand, the larger New Forest bogs show a very rich flora, numerically greater in species than any other bog areas of comparable size in Britain. *Myrica gale* is an abundant species in these bogs in all except the wettest Zones 1 to 3, as it is in Norfolk, but not (except rarely) in the Bagshot or Greensand areas of the south east. *Malaxis* is apparently more plentiful in some of these bogs than elsewhere in Great Britain to-day, while *Drosera anglica* occurs in plenty with the other two British species of the genus. It is otherwise absent to-day from S.E. England south of the Norfolk–Suffolk border fens. *Carex limosa*, a typical raised bog pool species, shows a similar distribution, and the Atlantic species *Pinguicula lusitanica* is common. *Schoenus nigricans* occurs locally in acid valley-bogs in Zone 3 areas in the New Forest and near Bagshot—it may represent a relic of former open fen conditions (see below under successions).

As to the bryophytes, the *Sphagnum* species present in all but the most recently formed bogs show much uniformity, except for *S. magellanicum*, which is much more local and absent from many Surrey, Sussex, Kent and Norfolk bogs, though there seems no evident reason for this. However, the writer has never observed capsules on this species in Britain. *Leptocarpus anomalus*, generally in Britain and North-west Europe the most abundant and constant hepatic in all *Sphagneta*, is extremely rare in the New Forest, where its place is largely taken by *Odontoschisma sphagni*.

BIOTIC FACTORS AFFECTING THE VEGETATION.

These can be classified under the headings of :—

- (1) Drainage.
- (2) Peat cutting.
- (3) Burning.
- (4) Grazing.
- (5) Planting of trees.
- (6) Disturbance due to military manoeuvres.

(1) *Drainage.*

In the past, much bog and heathland has been cleared and drained in certain parts of S.E. England and many bogs have vanished through this cause (e.g. Gamlingay Bog in Cambridgeshire), but the great majority of the existing heathlands where these bogs occur have been little interfered with by recent drainage operations, except in a few cases where wet heathland has been trenched prior to tree planting, particularly in east Dorset. This trenching leads, naturally, to a lowering of the water table and replacement of *Sphagnum* communities by *Molinietum* (*Molinia* is almost universally present, though as weak scattered individuals in undrained bog areas) or *Callunetum*.

In 1951 large new drains were observed in parts of two deep New Forest bogs, Wilverley Bog and Cranes Moor. It is too early to say what the final effect of these will be. In the more or less liquid peat of these bogs there will undoubtedly be a tendency for the drains to fill up with debris. It has been noticed already at Wilverley, however, that the *Sphagnum* carpet shows signs of dying very near to the drain, but not further than about 10 metres away.

In raised bog areas, drainage, as is well known, can be very effectively carried out, and one good example of this can be seen at Holme Fen in Hunts. where the drainage of the adjacent Whittlesey Mere in the eighteen-fifties, together with the cutting of drains across the raised bog, has led to the replacement of *Sphagnetum* by an *Erica tetralix*-*Calluna* heath with heathland mosses instead of *Sphagna* beneath this layer. Strangely, although the water table in summer is now at least 6 feet below the surface, *Cladium mariscus* (apparently a relic from the earlier fen stage which preceded the raised bog), survives vigorously in 'islands' among the heath vegetation.

At Chartley Moss, the eastern half of the bog has been drained by ditches, more effectively the further east one goes from the remaining undrained *Sphagnetum*, since the surface rises on to the sloping mineral ground in this direction. The area least affected by drainage on the margin of the *Sphagnetum*, bears *Eriophorum vaginatum* as a dominant (this is abundant in the undrained *Sphagnetum*) with *Betula pubescens* and heathland mosses (e.g. *Pleurozium schreberi*) on the peat surface. Farther east, *Molinia* becomes abundant among the *Eriophorum*, and in the driest part there is a *Betula* scrub in *Molinietum* with *Eriophorum vaginatum* still abundant. The S. African alien moss, *Orthodontium lineare*, is becoming abundant on dry peat and birch stumps in drained lowland raised bogs all over Northern England.

(2) *Peat cutting.*

This is of little importance in most valley-bog areas, as the peat generally is too fluid and too little humified to be of value for use as fuel or even to cut at all, but locally in the New Forest it seems to have occurred. Mr. P. Newbould, of the Nature Conservancy, is investigating this and many other historical factors in his intensive studies at Cranes Moor bog in the New Forest. In raised bog areas in Somerset and the Northern British lowlands, it is of course a very important factor in modifying the vegetation. Where such cuttings have occurred at Holme Fen, this has resulted in a putting back of the succession; fen communities reappear, followed by reinvasion of *Sphagnum* species of the fen colonist type (*S. squarrosum*, *S. subsecundum*). At Chartley Moss and Wybunbury Bog, no important peat cutting has occurred. If cuts are shallower, as in parts of the Somerset peat moors (and incidentally, in some German raised bogs) the mineral soil water table ('*Mineralbodenwassergrenze*') may not be reached, and then the colonization starts off with *Rhynchospora alba*, *Drosera* spp., and *Sphagna*.

(3) *Burning.*

The occurrence of fires is, as is well known, a frequent, not to say dominating factor, on the dry south-eastern heaths. In times of severe drought they often spread into the peat of Zone 5 areas, and over the surface (and even occasionally into the peat) of Zone 4 areas. This results in changes of a more lasting character than with merely superficial fires. The locality at which these phenomena have been most studied by the writer is Hothfield Common in East Kent. Here superficial fires in Zone 6 areas merely lead to a regeneration of the heath community in which development *Erica tetralix* assumes a temporary dominance, though later *Calluna* re-establishes itself from seed. The associated bryophyte flora however may be destroyed and evidently this takes a long time to re-establish itself. In Zone 5, the same may happen, but more severe fires destroy the rhizomes of *Erica tetralix* and the *Calluna* seeds in the surface litter while leaving the small *Molinia* tussocks in large part unharmed, as the meristems are so well protected by the mass of shoot bases. *Molinietum* of a vigorous tussocky nature then often supervenes. Deeper seated fires (such as the one at Hothfield in the drought summer of 1949, which burnt out the peat down to mineral soil level in a belt right across the centre of the main valley-bog, and smouldered for six weeks) have much more dramatic effects. Everything alive was destroyed in the area of the Hothfield fire, and a 'cliff' of unburnt peat, 9 inches high, bordered the edges of the burnt area. By April 1950, the layer of reddish ash left by the fire had become blackish in colour, and was extensively colonized by moss protonemata. By August 1950, it was richly carpeted in all the visibly damp parts with *Ceratodon purpureus* and *Marchantia polymorpha*. The latter species was a most remarkable sight, and bore an abundance of male, or female, receptacles. The drier areas of ash were devoid of any vegetation (even in 1952 some of these areas are still in this state). Over all the areas where there was any appreciable moisture (former Zones 4 to 6), great quantities of *Chamaenerion angustifolium* and *Polygonum lapathifolium* appeared. In July 1951, seedlings of *Molinia*, *Erica tetralix* and *Calluna* began to appear in small numbers, and this year were more plentiful. *Marchantia* is decreasing. It now appears as if in time, as the nitrogen, potassium, and iron released by the fire are leached away, the acid peat layer will be re-established and some sort of wet-heath community will develop. In the burnt areas, occupied formerly by Zones 1 to 3, pools of water accumulated after the winter rains, and various marsh plants have appeared, most of which were present in Zones 1 and 2 before the fire. These appear to have been stimulated by the extra nutrient supply following leaching of the ash on the slopes, and show vigorous growth.

It is noteworthy that *Narthecium ossifragum* has shown a great increase in vigour in the unburnt upper part of Zone 3, and also on the merely superficially burnt slopes (Zones 4 and 5) on either side. In Zone 3, this may be due to the better temporary supply of nutrients released by the burning of the slopes. In Zones 4 and 5 the increase in vigour is more marked, as till the first recent fires in March 1948, *Narthecium* was merely abundant here (four to twelve erect shoots per square foot), among a closed *Sphagnum* carpet under *Calluna* and *Erica tetralix*, and consisted of short shoots with orange-green leaves. Now it is becoming dominant (over fifty erect shoots per square foot in places) and has taller shoots with luxuriant green leaves. This may be a nutrient effect, or possibly due to removal of *Sphagnum* competition (the *Sphagnum* was in great part killed by the surface burning, as its live apices are very vulnerable when dry). It may be due to both factors in part. A similar effect has been observed at Chobham in Surrey. Here one unburnt Zone 3 area has moderately abundant *Narthecium* among *Sphagnum*, while an adjacent superficially burnt area has vigorous dominant *Narthecium* growing over dead *Sphagnum*, which is rapidly covered by the dead leaves of the *Narthecium* each autumn, as it can no longer grow through this carpet.

Experiments in growing *Narthecium* seeds were attempted in the laboratory in 1952. Fifty fresh seeds were sown on sterilized sand washed with HCl and glass-distilled water in each of three clean porous dishes. One was watered with glass-distilled water, one with 1 per cent KNO_3 solution, and one with 1 per cent K_2CO_3 solution. Germination in all three cultures was excellent, but the cultures became contaminated and were abandoned. It is hoped to repeat a similar experiment with mature rhizomes and measure the rate of growth.

(4) Grazing of Animals.

This factor can be subdivided into two main effects:—

(a) Cropping alone, as happens with rabbit-grazing.

(b) The trampling and manuring associated with grazing by cattle.

(a) The wetter parts of valley-bogs are carefully avoided by rabbits, who dislike getting their feet wet, though they like to sit on *Sphagnum* or *Polytrichum commune* hummocks, as is obvious from the piles of their droppings on such hummocks at times. They will not normally attack the mature closed stands of *Erica* or *Calluna* in the heath Zones 5 to 8. Tender young seedlings of *Calluna* or new shoots from rhizomes of *Erica tetralix*, however, are frequently nibbled down during regeneration after fires, and if attack is very heavy, this may check the succession. It has been noticed at Hothfield that *Calluna* is eaten in preference to *Erica tetralix*—in fact, seedlings of *Calluna* among *E. tetralix* are definitely avoided in preference to those which are not so surrounded. Rabbits will also eat the shoots of seedlings of trees (*Quercus*, *Betula* and *Pinus* in particular) which may colonize the heath zones, and so help to check succession to woodland. On the whole, however, rabbits do not appear to be very important agents in modifying the vegetation of the bogs in the more restricted sense.

(b) Nowadays cattle are not often allowed to graze with any high degree of intensity in bog areas; probably this is considered dangerous, and in any case the grazing of domestic animals on heathy common land is a practice which has largely died out in the Southern English lowlands, except in the New Forest. There the 'density' of cattle per unit area is not, it appears, enough to have much effect, and they confine themselves largely to the grass-heath areas anyway. There is, however, one small common in east Kent (Gibbon's Brook) which formerly, to judge from present relics and past floristic records, bore a fairly typical valley-bog association. Nowadays, however, a fair-sized herd of cattle tramples freely over the whole area, and also over the course of time spreads dung over an appreciable part of its surface. The trampling results in the breaking up of the remaining *Sphagnum* carpet, the grazing in the destruction of the small ericaceous shrubs, and the manuring in the alteration of the soil acidity and nutrient status. The former bog, though it still contains patches of *Sphagnum* and bog pools, is now largely converted into marsh, with the change from an oligotropic to a mesotrophic environment which this involves. The moss *Acrocladium cordifolium* is now one of the commonest bryophytes, and *Deschampsia caespitosa*, *Holcus lanatus*, and *Juncus effusus* are becoming important local dominants.

(5) Planting.

Deliberate planting of conifers has been observed in wet-heath communities in East Dorset and in Kent, and leads to a drying out of the surface with increase in vigour of *Molinia* and *Calluna*.

(6) Military Manœuvres.

The disturbance due to wartime and also post-war operations by tracked vehicles has been immense on many heathland areas in southern England, but only occasionally are the bogs themselves affected. At Hothfield Common,

tank runs across the bog have filled with water and bog pools, of a type similar to those already in existence on the bog, but larger, have developed, showing a characteristic hydrosereal succession. This starts with colonization of the open weakly acid but base-poor water (pH about 6.4) by *Potamogeton polygonifolius* and then by *Juncus bulbosus*; then *Campyllum stellatum*, *Hypericum elodes* and *Sphagnum cuspidatum* become abundant, followed by *Sphagnum pulchrum* or *S. plumulosum* with *Anagallis tenella*, *Scutellaria minor*, *Carex demissa*, and *Eriophorum angustifolium*. The water edges bear zones of *Aneura pinguis*, *A. multifida* and *Calypogeia trichomanis* in successively higher sequence of level. (This bog has a far less acid water supply than some (pH 6.4) which may account for its admixture of fen species.) Bomb craters show a similar succession.

pH PHENOMENA.

pH measurements were made colorimetrically with a BDH capillator set in all cases, but one series was checked electrometrically (see below). In general, the acidity of the soil water draining into lowland valley-bogs is not high, though the water is usually poor in nutrients, especially metallic cations, as is natural from the character of the parent rocks, usually base-poor sands. The water of the central rill at Hothfield Common bog (on Folkestone Sand) gave a pH reading of 6.4 (July 1952), that of the feeder stream at Louisa Lake Bog, Bedgebury, Kent (on Ashdown Sand), one of 6.2 (October 1951) and that of a spring on Ashdown Forest, Sussex (Ashdown Sand), which lower down became the central stream of a valley bog, one of 7.0 (December 1951). The water of pools in the hummock complex tends to be far more acid, as much of this water has been in contact with the acid-forming *Sphagna* of the hummocks. At Thursley Common, the water of pools with *Sphagnum cuspidatum*, etc., showed a mean pH of 4.9 in September 1951. Similar pools at Bog Common, W. Sussex, showed a pH of 5.8 in September 1951; and at Roydon, W. Norfolk, 5.2 in July 1951. The pH is usually higher below the surface, apparently due to reducing conditions.

Of greatest interest, however, are two points:—

1. The tendency of each *Sphagnum* species to develop a specific pH in the water contained in the hyaline cells;
2. The seasonal variation in pH of *Sphagnum* carpets or hummocks at any one locality.

This can be shown by the following table (fig. 3), prepared from data obtained at Bog Common, west Sussex. It would have been desirable to make pH

Bog Common, W. Sussex.	<i>Sphagnum</i> sp.	9 September 1951	7 January 1952
	<i>S. compactum</i>	4.2	5.3
	<i>S. tenellum</i>	4.4	5.4
	<i>S. rubellum</i>	4.5	5.7
	<i>S. papillosum</i>	4.5	5.9
	<i>S. pulchrum</i>	4.9	5.9
	<i>S. cuspidatum</i>	5.8	5.2
	<i>S. palustre</i>	4.1	5.2
	<i>S. recurvum</i>	4.1	5.8

FIG. 3.—pH figures (colorimetric) obtained from water squeezed from *Sphagnum* species at Bog Common, W. Sussex, in summer and winter.

readings at regular monthly intervals during the course of a year, but this was not practicable. Fairly warm, dry weather preceded the first readings (1951), while those of 1952 were made after a wet, cool period.

A similar set of readings was taken at Thursley Common bog, and is given below (fig. 4).

Ockley Bog, Thursley Common, Surrey.	Habitat	<i>Sphagnum</i> species	September 22. 1951	24 March 1952
	Hummocks	<i>S. rubellum</i>	3.8, 3.9, 3.9	4.6
		<i>S. magellanicum</i>	3.9, 4.2, 4.6	4.9
		<i>S. tenellum</i>	4.4	4.8
		<i>S. papillosum</i>	4.0, 4.1, 4.2	4.7
	low 'turf'	<i>S. pulchrum</i>	4.6	4.8
	Pools	Water from pools with <i>S. cuspidatum</i>	4.9, 4.9, 5.0	4.9, 5.0, 5.0

FIG. 4.—pH figures (colorimetric) obtained from water squeezed from *Sphagnum* species at Ockley Bog, Thursley Common, Surrey.

It will be noticed that the pH of the water in the hummock-*Sphagnum* tends to be less acid in winter and early spring than at the end of the summer, while in the pools of the bog there is no well-marked difference at different times. To understand the probable reasons for this phenomenon, it is necessary to refer to the work of Skene (1915), in which much information on the mechanism by which *Sphagnum* produces acidity is given. *Sphagnum* is there shown to possess a colloidal adsorption-mechanism in its cell-walls, which will remove metallic cations from a solution of any salt bathing the tissue, while leaving the anions in solution. The result of this is that water molecules dissociate, OH ions are apparently attracted to the adsorbed cations, and an increase occurs in the hydrogen-ion concentration.

The ability to adsorb cations is a character which shows quantitative variation according to the species of *Sphagnum* concerned, so that each species tends to produce a definite degree of acidity in dilute natural waters. The degree of acidity produced in each case (i.e. the pH) tends to be that which provides the optimum environment for the metabolism of each species. During active growth, the cations adsorbed are removed and used by the *Sphagnum*. In winter, when growth of *Sphagnum* is very slight or ceases, the cations accumulate (since this process is independent of vital activity and will occur with dead *Sphagnum* tissue), and thus the ability of *Sphagnum* to control its pH is reduced, as the cell colloids become saturated with cations. Now if, in addition, there is much rain with no subsequent evaporation, as happens in a cool temperate winter, a process of leaching-out of the hyaline cells is likely to occur, and the highly acid water will be replaced or diluted by rain water, which has only a slight acidity due to dissolved CO₂. We should therefore expect to find, and do indeed find, that the acidity of the *Sphagnum* hummocks falls. On the other hand, the acidity of the pools, and the *Sphagnum* in or beside them, should tend to remain fairly constant, as both acid-leachings and rain water will accumulate here. This also proves to be true.

In the next table (fig. 5) some figures for pH values obtained for the same samples of solution by both colorimetric and electrometric (glass electrode) methods are quoted.

There is seen to be fairly good agreement between these (admittedly few) pairs of readings. The colorimetric method gives a slightly higher value in

each case for the pH figure than the electrometric method. The pH values obtained in valley-bogs in general tend to be less acid than those in raised bogs, but flat bogs of relatively large size, as Thursley, Chartley Moss, and Wybunbury Moss, tend to show high hummock acidities comparable with those of the hummocks of raised bogs. In the central fen areas of the larger valley-bogs, where there is usually some water movement, pH values between 5 and 6 are usual ; while in those bogs where the central fen receives calcareous drainage-water, the pH may rise above 7 (Roydon Common 7.3, Buxton Heath 7.4, Bryant's Heath 7.0, Holmsley flush 7.6), due to free CaCO_3 in solution.

From top to base of a single *Sphagnum* hummock, great changes in pH may occur. At Louisa Lake, near Goudhurst, Kent, on 11 October 1951, a hummock of *Sphagnum recurvum* showed a pH of 4.4 at the living apex, and of 6.0 in the standing water at its base. A rill of moving water a yard away flowing into

Hothfield Common Bog, E. Kent. 11 July 1952.

Samples	pH (electrometric)	pH (colorimetric)
Water squeezed from tuft of <i>S. papillosum</i>	5.1	5.2
Water squeezed from tuft of <i>S. rubellum</i>	5.2	5.6
Water squeezed from tuft of <i>S. pulchrum</i>	4.3	4.4
Water from stagnant pool	6.0	6.3
Water from slow- moving rill in bog	6.2	6.4
Water squeezed from <i>S. compactum</i> on wet heath	5.2	5.6

FIG. 5.—Comparison of colorimetric (B.D.H. comparator) and electrometric (glass electrode) pH values obtained, using the same samples of solution in each case.

the lake had a pH of 6.2, while that of the lake itself was 6.6. For the above reason, it is important when talking of pH in *Sphagnum* hummocks, to be quite sure exactly to what part of the hummock we refer. All the pH readings previously quoted for non-aquatic *Sphagna* refer to water squeezed from the living apices of the shoots. Where *Sphagnum* (especially *S. plumulosum*) is invading stagnant open calcareous fen (e.g. Roydon Fen, E. Norfolk), still more dramatic gradients of pH can be seen ; from 8.2 in the soil water below a *Sphagnum* hummock, to 6.5 at the top in March 1952.

SUCCESION IN VALLEY-BOGS.

The seral phenomena associated with valley-bogs are varied and sometimes complex, and here it is only possible to indicate the most important features.

As already noted, soligenous valley-bogs can develop either (i) directly over lakes or ponds as part of a primary hydrosere, when the conditions are sufficiently oligotropic, or else secondarily over (ii) fen or swamp, or (iii) even-felled woodland. Examples of development of these types have been studied in several places. Information has been obtained both from present-day successions and from stratigraphical examinations of older bogs.

DEVELOPMENT OF BOGS OVER LAKES.

In Minnesota, according to Conway (1949) flat bogs showing this type of development are characteristic. There a floating 'pioneer-mat' community grows out over the water from the edges, composed of such species as *Carex lasiocarpa* and *Typha latifolia*, followed by a 'moss-heath' community, in which *Chamaedaphne calyculata* is the dominant dwarf shrub, associated with *Andromeda glaucophylla*, *Oxycoccus quadripetalus*, *Sphagnum recurvum* and *S. magellanicum*.

Finally a 'bog-forest' is initiated by *Larix laricina*, and develops via either *Picea mariana* or *Thuja occidentalis* forest to a climax of *Abies balsamea*. A type of succession, similar in structure, though with different species involved, can be seen in Great Britain; particularly round the Cheshire Meres, but also in the South of England. An excellent example is to be seen at Louisa Lake, nr. Goudhurst, Kent. Here an artificial lake about 40 m. wide by 80 m. long lies amid deciduous woodland, on soil derived from the loamy base-poor sands of the Hastings Beds. The lake still has an area of open water about 15 m. long by 10 m. wide at its lower end against the dam; but the rest of its area is now filled with a series of zoned 'floating-mat' plant associations which represent an interesting oligotropic hydrosere. These are as follows (see fig. 6):—

- (1) Open water with *Potamogeton polygonifolius*.
- (2) Swamp with *Equisetum limosum* d.
- (3) Mat of *Eleocharis multicaulis* and *Hypericum elodes* co-d; *Equisetum limosum* still abundant.
- (4) *Sphagnum subsecundum* d, in a floating carpet with *Eleocharis* and *Hypericum* abundant; *Equisetum* still present.
- (5) Mat of *Sphagnum subsecundum* d, and *Molinia* (scattered tussocks).
- (6) *Sphagnum palustre* hummock association with *Erica tetralix* abundant on the hummocks; *Molinia* abundant between them and small willows and birches.
- (7) Mineral ground with *Calluna*, *Erica tetralix*, *Sphagnum palustre* and dense birch scrub. A hole was made in Zone 6 and dead *Equisetum limosum* stems were found beneath indicating the succession that had taken place (fig. 6).

Elsewhere the successions that have occurred have been studied by means of borings or by holes dug through the surface of the bogs (see fig. 7).

At Thursley Common (Ockley Bog) in Surrey, the surface carpet of living *Sphagnum papillosum* in the bog centre is underlain by a foot or more of dead *S. papillosum* remains, scarcely humified at all, and little compressed. As one goes downwards, *Eriophorum angustifolium* (which is frequent to abundant as a living plant on the surface) becomes more plentiful, until the lowest part of the 'peat' profile is entirely composed of its remains below about 1 foot 3 inches. Finally, at from 1 foot 9 inches to 2 feet down, a layer of black peaty mud about 1 inch thick occurs, and below this grey muddy sand. The whole 'peat' profile above the mud is soup-like in consistency and smells strongly of H_2S .

This bog evidently commenced relatively recently as a shallow lake, which became invaded by *Eriophorum* swamp and then by *Sphagnum papillosum* (or, over part of the area, *S. pulchrum*).

At Wilverley Bog in the New Forest, the present *Sphagnum* carpet has very numerous scattered shoots of *Phragmites* near the margin of the swamp Zone 2. These are unhealthy looking and frequently attacked by gall-forming insects. A hole made through a *Sphagnum magellanicum* hummock in the main *Sphagnum* Zone 4 showed:—

25 cm. loose *S. magellanicum* remains above the water table.

20 cm. *Sphagnum magellanicum* peat below the water table, with remains of *Juncus sylvaticus* (not now present alive at the surface at this point in the bog).

5 cm. of sludgy peat with *Alnus* wood and *Juncus* remains.

10 cm. of mud and *Juncus* roots with stones.

Then gravel.

Other borings nearby in the area where *Phragmites* was frequent showed abundant remains of *Phragmites* below the surface, reaching down to 30 cm. below the water table in sludgy peat.

This appears to indicate that, at Wilverley, swampy fen became established over a mud bottom and later developed locally alder carr, which for some reason became overwhelmed by *Sphagnetum*.

Elsewhere in the bog, the top of the fen-peat layer bears a thin gravel layer, with c. 30 cm. *Sphagnum* peat on top, suggesting a phase of soil erosion (? due to forest clearance) followed by establishment of *Sphagnum*.

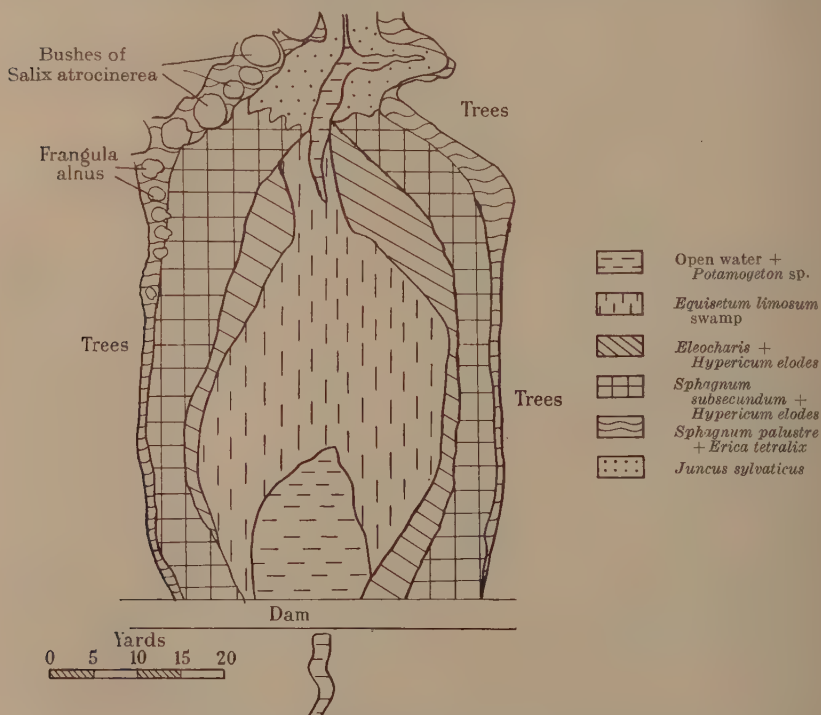


FIG. 6.—Louisa Lake, Bedgebury Forest, near Goudhurst, Kent, to show hydrosere development.

At Roydon Common, West Norfolk, a similar open *Sphagnetum* with scattered weak stems of *Phragmites* and sterile *Juncus subnodulosus* is found near the centre of the valley-bog. Beneath the *S. papillosum* carpet (pH 4·8) the water table was 10 cm. below the surface (pH 5·2) and below this was 50 cm. of semi-liquid black peat, with many dead *Juncus subnodulosus* rhizomes (above) and dead *Phragmites* shoots (below). Some of the living *Phragmites* and *Juncus* shoots were still attached to dead rhizomes, deeper down.

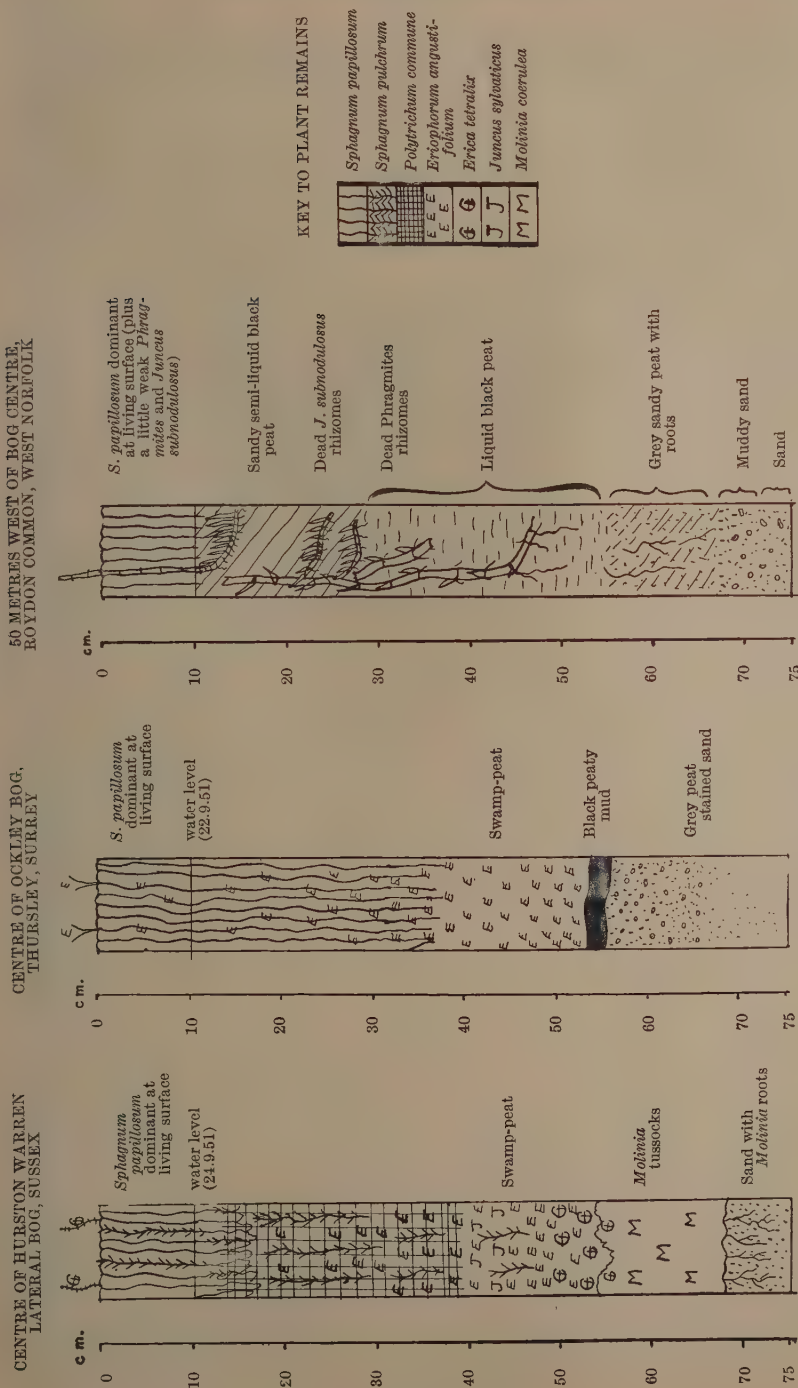


FIG. 7.—Peat profiles at three southern valley-bogs to show types of succession

Below 60 cm. from the surface was greyish sandy peat with roots to 68 cm. then muddy sand with roots to 70 cm. Evidently here a *Phragmites-Juncus* fen has been recently invaded by *Sphagnum*. Indeed, Zone 2 here is still in part open and calcareous (pH 7.3) in the pools, though *Sphagnum* invasion proceeds.

At Hurston Warren, W. Sussex, a tract of several acres of open *Sphagnetum*, in part of Zone 3 (central) and in part of Zone 4 (marginal and above) occurs in a side valley to the main valley of the River Chilt. The level of the *Sphagnum* surface in the side valley is about 2 feet above that of the *Sphagnum* surface of the main valley, and there is a similar difference in the levels of the water table in the main valley and side valley. The reason for this phenomenon is the existence of a clearly artificial bank across the mouth of the side valley which appears to have carried an old trackway and acts as a dam. Though the vegetation of the side valley bog has developed a rich flora of vascular plants and hepatics, this may be due to its proximity to the older bog in the main valley, rather than to its age. The stratigraphy suggests a relatively recent development of this bog, and local enquiry suggests it has become much 'wetter' within the last 50 years, though as is usually the case, precise information is lacking from local sources. A hole was made near the centre of the side valley. Beneath the generally dominant *S. papillosum* of the surface, the water table is reached about 4 inches (10 cm.) down. *S. papillosum* remains occur down to about 17 cm.; while *S. pulchrum*, occurring as scattered stems at the surface, becomes abundant as remains below 15 cm., as does *Polytrichum commune*, only found very locally at the surface at present, so below 17 cm. down to c. 30 cm., the fluid 'peat' contains mostly *Polytrichum commune* and *Sphagnum pulchrum*. Below this, *Eriophorum angustifolium* remains are abundant (only abundant in pools at the surface today) in watery 'peat' with *Juncus sylvaticus* and *S. pulchrum* down to 55 cm. Below 55 cm., there is a dramatic change to a layer of *Erica tetralix* shoots and a dense mass of *Molinia* tussocks, beneath which at 68.5 cm. the sandy mineral soil is found. It would seem that a *Molinia-Erica* damp heath association existed before the valley was dammed up; the construction of the raised causeway led to the flooding of the side valley, the drowning of the *Molinia* heath and the initiation of an *Eriophorum-Juncus* swamp, with some *Sphagnum pulchrum*. This became invaded by *Polytrichum commune* hummocks, and these in turn, were overwhelmed in most places by *Sphagnum*, mostly *S. papillosum*, locally *S. pulchrum* in the deeper central part. It is a pity an exact date cannot be fixed for the construction of the causeway.

In the main valley below the 'dam' at Hurston, *Molinietum* is heavily invaded by *Polytrichum commune* and *Sphagnum papillosum*. An old ditch in the bog, now filled with *S. pulchrum*, suggests former efforts at drainage. Indeed, beneath the *Molinietum*, *Sphagnum pulchrum* occurs in the peat in abundance.

It appears that here an original Zone 3 *Sphagnetum* was replaced by *Molinietum* on drainage, then as the drains have become choked up, *Polytrichetum* and *Sphagnetum* have supervened. Similar replacement of *Sphagnetum* by *Molinietum* on partial drying out (not necessarily due entirely to human interference) can be seen at Holmsley and Wilverley Bogs in the New Forest, and Morden Decoy bog in Dorset.

The general tendencies in valley-bog succession would appear to be the replacement of swamp-communities by *Sphagneta*, the raising in level of these till *S. rubellum* hummock development occurs over *S. papillosum* (demonstrated in numerous cases). Finally it seems *Molinietum* may develop on the drying *Sphagnum* surface, as the liquid peat below finally gets compacted and thus the weight of the *Sphagnum* carpet and hummocks can no longer continue to force the living surface carpet down to near the water table. One can note

from cuttings the more solid nature of the peat at Holmsley and Wilverley in the areas where *Molinia* tussocks have overwhelmed the *Sphagnum* hummock complex. Certainly the *Molinia* was much more truly dominant at Holmsley in 1952 (covering the whole open bog except for the pools and drainage runnels), than it was on my first visit in 1938, when much of the bog was open *Sphagnetum* and far wetter. This change presupposes no pioneer invasion of *Molinia* into the *Sphagnum*, because *Molinia* is almost invariably present in the *Sphagneta* of lowland valley-bogs, in every square metre, or even every square foot, as transects and quadrats have indicated.

There is little tendency to woodland development except in the better flushed and aerated central parts of the larger valleys. It is not that seeds of trees do not arrive, and cannot germinate in the acid *Sphagnum* carpets; small one- or two-year seedlings of birch and oak are very common in the bogs, being almost constantly seen wherever woodland is at all near (within a quarter mile), and pines are quite frequent. Oak seedlings, indeed, are more plentiful in wet *Sphagnetum* than on drier heathland nearby. At Kingsley Common, N. Hants, in September 1951, seven oak seedlings were found in a 10 square yard plot of dry peaty heath (Zone 7), and 26 in a 10 square yard plot of damp heath (Zone 6) adjoining.

No doubt germination is better in the wetter places. But the seedlings usually do not survive a second year and deciduous trees of any size are absent in wet *Sphagnetum*, though birch can invade *Molinietum* and Zones 8 to 5 fairly readily. *Pinus sylvestris* is a more successful colonist and can grow for a number of years on well-drained *Sphagnum rubellum* hummocks, and in Zone 5 (wet-heath). The trees, however, are always stunted and develop short needles reminiscent of var. *scotica*, as pines do on raised bog. Trees of 15 years old, only a yard high are frequent. This is well seen at Thursley, Wilverley, Chartley, Wybunbury, and about Bagshot.

The replacement of *Alder* carr by *Sphagnetum*, which has evidently occurred at Wilverley, Cranes Moor, and elsewhere, needs more explanation.

Mr. P. Newbould of the Nature Conservancy has made an interesting suggestion about this point, and I am indebted to him for the theory. He points out that deforestation in the New Forest in the past must have involved the conversion of large areas of woodland on the higher ground into heath; and consequently must have reduced the water-retaining properties of the uplands. The greater run-off of water would cause undue swamping of the valley alder-woods and the onset of more anaerobic conditions for their roots, thus causing their death and replacement by *Sphagneta* or swamp vegetation.

SUCCESSION LEADING TO DEVELOPMENT OF VALLEY BOGS ON HEATHLAND WITHOUT PRIOR FEN DEVELOPMENT.

In general, lowland valley or soligenous bogs are confined to those parts of Britain where the surface rock consists of sands, sandstones or gravels which form light porous soils poor in bases, and, in the British climate, readily podsolize when under coniferous or ericaceous vegetation.

The very porosity of these soils is, paradoxically, one of the reasons why they tend to become waterlogged and to produce bogs locally. Where these rocks giving rise to light base-poor soils were present, early man found it apparently easier to clear the forest (which must have occurred previously over nearly all the British lowlands) than on heavier clay soils. This clearance must have occurred presumably by Bronze Age times, as round barrows or tumuli of that period are frequent on very many of our southern heaths, and presumably were not built in forest (but see Tansley, 1939, p. 164). Following on clearance, heathland must have developed subsequently and been maintained by fires and grazing in a fairly open condition.

After a time the porous soil and the evergreen heath vegetation between them would have resulted in podsolization of the surface.

The B2 horizon (iron pan) or the podsols formed would tend to hold up water on concave, or even flat, ground surfaces, and damp-heath (or even wet-heath) might develop on quite level areas of heathland plateau (which has occurred for example at Lavington, Iping, Ambersham and Heyshott Commons, W. Sussex).

Concave surfaces, however, would tend to receive extra drainage water from a larger catchment area, and thus, at the lowest parts of such depressions, there would be available the more permanent moisture supply required by hummock-forming *Sphagna* (such as *S. papillosum* and *S. magellanicum*). The shelter from desiccation provided by the *Calluna-Erica tetralix* sward above, and the sponge-like water-holding properties of the wet-heath *Sphagna* already established below would enable these hummock *Sphagna* to become established, as has actually happened at Heyshott Common (bog no. 3).

We can summarize the successional phenomena theoretically as follows (fig. 8).

DISCUSSION AND CONCLUSIONS.

The structure of various types of valley-bogs, their differences from raised bogs, and their development have already been discussed, and the ultimate type of climax likely to be developed has also been considered.

It remains for us to consider :—

(i) the reasons why bogs of this type are a feature of only *certain parts* of Britain (and of Western Europe as well) ;

(ii) why raised bogs do not always occur in the same districts ; and

(iii) what is the real difference in the ecosystems involved in raised and valley-bogs ?

In the first place it is necessary to be clear about our terminology. The word ' bog ' is here used to indicate any type of peat mire with some species of *Sphagnum* largely dominant in the field layer (which contributes the major part of the bulk of the immediate substratum), and with a fairly acid ($\text{pH} < 5.5$) reaction over the main parts of its surface. This would include various *Sphagnum*-dominated ' poor-fens ' in the Swedish sense (see above, p. 188). The word ' fen ' as here understood by me means any association on wet peat, whether alkaline, neutral, or slightly acid, in which non-ericaceous angiosperms form the bulk of the vegetation, and *Sphagnum*, if present, plays only a very subordinate part in the structure of the field- or moss-layer. It is now possible to consider the three points above.

(i) Lowland soligenous bogs only occur in regions where there are areas of rock which are both porous physically and poor in bases (or at least easily leached of them) chemically. Permanent Zone 4 bog, as we have seen, requires for its development also the existence of certain topographical features, namely either (a) valleys which expose springy lines at junctions of pervious and impervious strata, or (b) depressions, in which lakes or swamps can develop, either through an initially impervious (often podsolized) floor, or through artificial damming and raising of the water table. If the rocks in an area are non-porous (which in lowland areas of England usually means that they are clayey or loamy), the denser deciduous woodland which is the natural climax of these more water-retentive and more base-rich soils might not have been cleared till much later than over the sands (see p. 207) and would then mostly have been cultivated. Even if left as woodland, podsolization and marked leaching would not occur, and any wet areas in valleys would not develop the open conditions needed for open bog *Sphagneta*, though in such areas, stagnant woodland type bogs with much *Sphagnum palustre* and *S. recurvum* may develop in hollows (e.g. below Leith Hill, Surrey). Where the soil is porous

but base-rich, as over chalk or oolite, fens will develop in valleys below the spring lines, but, owing to the regular supply of mineral salts in the drainage water, *Sphagnetum* is unlikely to develop unless conditions are (a) relatively stagnant, and (b) maintained relatively open by cutting or grazing of the luxuriant *Magnocaricetum* associations.

Open bogs in the lowland low-rainfall areas are therefore associated in every case with podsolized soils developed under heath or open heathy woodland on base-poor rock. If the base-poor sands or gravels form a surface layer only, with base-rich soils of more impervious nature below, the spring line at the junction of the pervious base-poor and impervious base-rich strata may well develop bog, as in the East Anglian examples cited above, but fen will be developed lower down, where the water supply is richer in bases. The development of soligenous bogs in low rainfall areas would also appear to be dependent on clearance at some past date, of the natural forest cover which appears originally to have existed on even the poorest and lightest sands and gravels. (See remarks on Wilverley bog above.) Hence the soligenous lowland bogs all show very recent *Sphagnum* development, though much older fen peat may occur beneath.

(ii) The development of raised bogs requires a heavier rainfall. At least 40 inches (about 1000 mm.) per annum is required in the cool temperate climate of north-western Europe. This is true as far inland as south Germany (Württemberg).

Relics of raised bogs occur to-day in Somerset (Shapwick), in Sussex (Amberley) and in Hunts (Holme, Woodwalton) but although these have all been drained, it is very doubtful if they would still be active in any case with the present rainfall. The ombrogenous peat growth was presumably initiated (as is known to be the case with some of these raised bogs) in the Atlantic period of higher rainfall. Both types occur together to-day in higher rainfall areas (e.g. Strathspey, West Inverness-shire) and in such conditions transitional stages may be seen from one type to the other. As Godwin (1939) points out, undisturbed raised bogs are long-lived structures, and an increase in rainfall may render a bog active again after a period of stagnation of growth.

(iii) It is fairly clear that raised bog development (i.e. above the plane of the mineral soil-water table—'Mineralbodenwassergrenze') requires a heavier rainfall than that of soligenous bog. What is less certain is how much of the water used by the growing *Sphagnum* in a raised bog comes (a) directly from rain on the surface, or (b) from below by capillarity. Du Rietz (1950 a and b) regards (a) as all important. Rigg (1940) is less certain. It may well be that where rainfall is relatively low, raised bog development requires water from both meteoric and telluric sources. A small experiment was carried out by the writer at Thursley in Surrey (rainfall c. 30 inches per annum). Glass plates, about 8 inches by 6 inches, were supported an inch above *Sphagnum rubellum* hummocks in the bog and left from January to March 1952. The *Sphagnum* remained fully wetted beneath even the centre of the plates where rain could not reach them directly. In summer, the hummock tops dry out slightly even when uncovered. A *Sphagnum rubellum* hummock was placed in a tin basin to prevent water access from below, and left uncovered. It remained fully wetted all through the winter of 1951-2 (November to April) and, indeed, the tin overflowed; but after April complete drying out occurred repeatedly. This experiment, of course, needs to be carried out on a larger scale, but it seems that in the present climate of S.E. England soil water is essential to keep *Sphagnum* constantly wet during the summer months (when most growth normally occurs: from 2 to 4 cm. per annum in *S. rubellum*). It is clear, however, that our lowland valley-bogs are essentially recent; perhaps even in the main, indirectly anthropogenic structures, dependent on forest clearance and on soil-water of low base-status (though not necessarily acid initially), for their development and maintenance.

ACKNOWLEDGMENTS.

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I should also like to thank Messrs. P. Newbould and M. E. D. Poore, for very useful discussions on aspects of bog ecology, in which field of research they are engaged.

REFERENCES.

- CLAPHAM, A. R. & GODWIN, H. 1948. Studies of the Post-Glacial History of British Vegetation VIII. Swamping Surfaces in Peats of the Somerset Levels. *Phil. Trans. (B)*, **233**, 233-249.
- CONWAY, V. M. 1949. The Bogs of Central Minnesota. *Ecol. Mon.*, **19**, 173-206.
- DU RIETZ, G. E. 1949. Huvudenheter och huvudgränser i svensk myrvegetation. *Svensk bot. Tidskr.*, **43**, 274-309.
- . 1950 a. Phytogeographical Mire Excursion to the Billingen-Falbygden District in Västergötland (Southwestern Sweden). 7 *Int. Bot. Congr. Stockholm* 1950, Excursion Guides, Uppsala.
- . 1950 b. Phytogeographical Mire Excursion to N.E. Småland and Östergötland. *Ibid.*
- . 1950 c. Phytogeographical Mire Excursion to the Ryggmossen Mire near Uppsala. *Ibid.*
- DU RIETZ, G. E. & NANNFELDT, J. A. 1925. Ryggmossen und Stigsbo Rödmosse, die letzten lebenden Hochmoore der Gegend von Uppsala. *Svensk Växtsoc. Sällsk. Handl.*, **3**, Uppsala och Stockholm.
- GODWIN, H. & CONWAY, V. M. 1939. The Ecology of a Raised Bog near Tregaron, Cardiganshire. *J. Ecol.*, **27**, 313-353.
- HARDY, E. M. 1939. Studies of the Post-Glacial History of British Vegetation, V. The Shropshire and Flint Waelor Mosses. *New Phys.*, **38**, 4, 364-396.
- OSVALD, H. 1923. Die Vegetation des Hochmoores Komosse. *Svensk Växtsoc. Sällsk. Handl.*, **1**, Akad. Avhandl. Uppsala.
- . 1948. Notes on the Vegetation of British and Irish Mosses. *Acta Phytogeogr. Suec.*, **26**, Uppsala.
- . 1950. The Raised Bog Komosse. 7 *Int. Bot. Congr. Stockholm* 1950. Excursion Guides, Uppsala.
- PEARSALL, W. H. 1941. The "Mosses" of the Stainmore District. *J. Ecol.*, **29**, 161-175.
- PETCH, C. P. 1945. The Vegetation of Roydon Common. *J. Ecol.*, **32**, 2, 143-46.
- RIGG, G. B. 1940. The Sphagnum Bogs of North America. *Bot. Rev.*, **6**, 666-693.
- SKENE, M. 1915. The Acidity of *Sphagnum* and its Relation to Chalk and Mineral Salts. *Ann. Bot.*, **29**, 65-87.
- SLEDGE, W. A. 1949. Distribution and Ecology of *Scheuchzeria palustris*. *Watsonia*, **1**, 24-35.
- TANSLEY, A. G. 1911. *Types of British Vegetation*. Cambridge.
- . 1939. *The British Islands and their Vegetation*. Cambridge.
- WATSON, W. 1915. A Somerset Heath and its Bryophyte Zonation. *New Phyt.*, **14**, 80-93.
- . 1932. The Bryophytes and Lichens of Moorland. *J. Ecol.*, **20**, 284-313.

PROCEEDINGS OF THE GENERAL MEETING HELD
24 April 1952

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 3 April 1952, having been circulated, were taken as read, and confirmed.

The PRESIDENT read a Message received from the Home Secretary in reply to the Address of Condolence sent to Her Majesty The Queen after the death of His Majesty King George VI, Patron of the Society.

Home Office,
Whitehall.

5th April, 1952.

Sir,

I have the honour to lay before The Queen the Loyal and Dutiful Address of The President, Council and Fellows of the Linnean Society of London on the occasion of the lamented death of His late Majesty King George the Sixth and have received The Queen's Commands to convey to you Her Majesty's grateful Thanks for the assurances of sympathy and devotion to which it gives expression.

I am, Sir,

Your obedient Servant,
David Maxwell Fyfe.

The President,
Linnean Society of London.

The following was thanked for a gift made to the Library since the last Meeting :—Mr. E. A. Bowles, F.L.S.

Mr. Denys Morgan signed the Obligation in the Roll and Charter Book, and was admitted a Fellow.

The PRESIDENT reported the deaths of Walter Samuel Millard, Fellow, Ole Theodor Jensen Mortensen, Foreign Member, and Frederick James Pittock, Associate *honoris causa*.

Certificates of recommendation for election of Fellows, Foreign Members and an Ordinary Associate were read for the first time in favour of the following : Fellows :—Mrs. Antoinette Nellie Gibby, B.Sc., H. E. Goto and Thomas James Walsh, Ph.D. Foreign Members :—Prof. Dr. Lothar Geitler and Dr. Ernst Mayr. Ordinary Associate :—Miss Olga Holbek.

The following candidates for Fellowship and Ordinary Associateship were balloted for and elected. Fellows :—John Patrick Micklethwait Brenan, M.A., Miss Kathryn Benson-Evans, M.Sc., Francis Jessop Bingley, M.A., A. J. Boerman, M.D., Dr. Margaret Elizabeth Brown, M.A., Prof. C. G. C. Chesters, Douglas Graham Cowden, B.Sc., John Heslop Harrison, M.Sc., Ph.D., Thomas Raeside Laycock, B.Sc., Aleksandrs Melderis, Ph.D., Mahmoud Ahmed Melouk, M.Sc., Ph.D., Francisco D'Ascensão Mendonça, Denys Morgan, B.Sc., S. K. Mukerjee, M.Sc., Ph.D., Mrs. Elsie H. Purnell, M.A., A. R. Ranjha, Prafulla Chandra Sharma, M.Sc., Mrs. Sybil Alice Stern, Kenneth Swinburne, Alasdair Ramsay Tainsch, M.B.E., B.A., Bernard Verdcourt, B.Sc., A.L.S., Owen Lynden Wade, M.A., M.D., M.R.C.P.(Lond.), A.L.S. and Derek Oliver Weitzel, B.Sc. Ordinary Associates :—John Frederick Bradbury, Lewis Leonard Forman, B.Sc., Stuart Stanley Kidd, B.Sc. and Miss Joan Valerie van der Smagt.

A Symposium on Form and Function in the Molluscs was held, which was opened by Prof. Alastair Graham, Dr. V. Fretter, Dr. J. E. Forrest, Mr. B. B. Boycott and Mr. J. E. Morton.

A general discussion followed, in which the following took part :—Dr. C. F. A. Pantin, F.R.S., Dr. Anna M. Bidder, Dr. A. Tindell Hopwood and Mr. W. E. Hollows ; Dr. Fretter, Mr. Morton and Prof. Alastair Graham replied.

FORM AND FUNCTION IN THE MOLLUSCS

By ALASTAIR GRAHAM.

In introducing a symposium on "Form and Function in the Mollusca" I think that the first point which should be made is that the selection of such a topic reflects a great change in the approach to the study of that phylum by zoologists. My recollection of lectures given to me as a student is of a portrayal of animals the bodies of which coiled and uncoiled—apparently as fancy took them—in a variety of planes in space, without much reference to the physiological effects which would accompany these changes, and the internal anatomy of which seemed to be made largely of a nervous system which, in gastropods at all events, criss-crossed in surprising fashion and which could not be found for checking purposes in one's dissections anyway.

To-day much of this is altered, and although malacology is still a rich field with many parts all but unexplored, it is now possible to give in one's courses of lectures some idea of the way in which the body of a mollusc works and of how its structure has come to adapt itself to the particular niche which it occupies in the living world. This change in the attitude of zoologists to malacology is associated with the work of two men whose names I should like to mention to you: Professor J. H. Orton and Professor C. M. Yonge. I think that it is largely due to their efforts that we now think first of the mollusc as a living animal and as a member of a community of living animals.

The original mollusc appears to have been a creeping animal probably of littoral or sub-littoral habits and all the evidence indicates that it had evolved from an ancestor with the organization of an animal belonging to the turbellarian-nemertine stock. It crept over the shore collecting débris of all sorts, but of microscopic size, by means of the radula set in the buccal mass in the anterior part of the gut. The material raked together in this way was swallowed and sorted in the stomach, an organ which has turned out to be one of the key organs in the functioning of the molluscan alimentary tract (Graham, 1949). The animals were enclosed within a shell for the protection of the visceral hump and mantle cavity and they shed their reproductive cells into the surrounding sea-water, where fertilization occurred.

In evolving from some such starting point the molluscs, and in particular the gastropods, have come to occupy an extraordinarily large number of ecological niches and in adaptation to this their body seems to undergo a more radical kind of transformation than does that of any other kind of animal. Only a few have retained the original microphagous habit: most have become accustomed to deal with larger masses of food either of vegetable or of animal origin. The paper by Morton (p. 240) shows how the stomach of some of these has become transformed in the process, whilst some of the problems which confront molluscs adopting a carnivorous diet are dealt with by Forrest (p. 225) and myself (p. 214). Of these carnivores only the cephalopods have become active swimmers with well developed sense organs: it is, therefore, not surprising that they are endowed with much more complex behaviour patterns than is any other kind of mollusc and, indeed, than are most types of invertebrate. Some of these are described in the paper by Boycott (p. 235).

At the same time as changes occurred in the diet and in the alimentary tract of the evolving mollusc, alterations occurred in their reproductive physiology. Change of some sort was essential for such as invaded brackish or fresh waters or land but was equally forced on littoral forms by competition; the main form which it took being the replacement of external by internal fertilization and the consequent development of copulatory organs. The molluscs are unique, however, in that copulation takes place by way of the

same cavity as acts as respiratory chamber, and between animals the bodies of which are enclosed within unyielding shells so that, mobile as they are, there is a limit beyond which further deformation of the body is prevented by the rigid shell. As a consequence a variety of methods of sperm transference has been evolved in the group and some of these are described in the paper by Fretter (p. 217).

Most people have their ideas as to what are the characteristic features of a carnivorous animal settled for them at an early age by childhood tales of lions and tigers, wolves and bears, and so come to think of a carnivore as always possessing the strength, intelligence and speed of action that mark those splendid creatures. They therefore find it difficult to conceive how such a group of animals as the molluscs, the habits of which have contributed the word 'sluggish' to the English language, can have the power to overwhelm other animals and use their bodies as food. It is, of course, true that the cephalopods rival the vertebrates and arthropods in keenness of sense organs, in intelligence and in the rapidity of their reactions—but they have come to resemble the more familiar carnivores only in so far as they have lost the typical molluscan characteristics. Apart from the cephalopod no mollusc appears to have been able to evolve that combination of acute sensory equipment linked by way of efficient nervous centres to rapidly acting effector organs which pre-judgment of the situation in the light of arthropod and vertebrate structure would seem to indicate was essential for the successful pursuit of the carnivorous way of life. How, then, is it possible for members of such groups of the Mollusca as the Gastropoda and Lamellibranchia to become carnivores when they are incapable of more than slow and ponderous movement with a nervous system of only modest capability? The answer is that, perforce, they have to rely on attacking animals which are still slower in their rate of movement than they are themselves, or which are completely immobile, or that they rely on the haphazard snaring of passing organisms. Prey of the first sort is usually armoured defensively with shells or tubes or spicules of a variety of sorts and presents a formidable exterior to the mollusc about to feed upon it: most of the adaptations of the carnivorous gastropods, in fact, are related to the necessity of overcoming these defences and to dealing with the vast quantity of indigestible and resistant material introduced into the alimentary tract rather than to any other aspect of their way of feeding.

Only a few molluscs feed by the method of trapping in some way such organisms as happen to come into sufficiently close proximity for this to happen. Since this is an essentially random method of feeding it is perhaps not surprising that these few are particularly marked by the sedentary nature of their life. The main group of the phylum which captures food in this way is that of the septibranch lamellibranchs, the feeding mechanism of which has been described by Yonge (1928). Here, by the sudden raising of the membrane fashioned out of the gills, water is sucked into the mantle cavity, bringing with it any small animals which happened to be in the neighbourhood of the inhalant siphon at that instant. These are now trapped within the mantle cavity and in this circumscribed space the feeble offensive organs of the bivalve are adequate ultimately to overcome the animal and push it through the mouth into the alimentary canal. A similar type of feeding mechanism is also to be found in such a carnivorous gastropod as *Vermetus gigas* (Boettger, 1930) which spins a net of mucus from the pedal gland into the surrounding water: small animals swim into this and become entangled in the sticky threads which are then rolled up and eaten.

Most carnivorous gastropods, however, actively hunt their prey. Of these the simplest cases are those of the nudibranch molluscs which browse on naked or relatively unprotected sessile animals such as sponges, coelenterates and polyzoans. Here the body of the prey may be guarded by spicules or

protective layers but it is never enclosed by a thick calcified shell. The body of the animal is therefore directly or almost directly exposed to attack and the food may be ingested at once into the gut of the predator, although it will almost certainly be mixed with some of the defensive material. A mollusc with such feeding habits has not been compelled to elaborate any kind of mechanism for crushing the shell of its prey either before or after eating it, and the gut of these nudibranchs is relatively simple with the breakdown of the food accomplished primarily by enzymatic action. In the case of dorids, which feed on sponges or polyzoans, the food is rasped by the radula and raked into the gut in familiar gastropod fashion, although Forrest (1950) has described in some, which feed upon polyzoans, a muscular suction pump attached to the anterior end of the gut, which helps to pull the zooids out of their protective coverings. The only other significant adaptation in the gut is a fairly extensive layer of cuticle over the anterior chambers to give mechanical protection against abrasion by spicules or similar defensive elements. Many of the nudibranchs, especially the eolids, which feed upon hydroids or sea-anemones, show a degree of physiological specialization which allows them to use such animals for food despite the abundance of protective nematocysts which they contain. Nematocysts are weapons not under nervous control which explode on contact, the explosion usually being facilitated by surface-active agents diffusing from the food (Parker & Van Alstyne, 1932). Their explosion may, similarly, be delayed or prevented by a reduction in the amount of surface-active agent or by the production of materials inactive in that respect, and it seems likely that mucus, which is secreted copiously over the hydroid or anemone which an eolid is about to attack, is such a desensitizing substance and is produced by the mollusc with that result.

In contrast to these gastropods the commonest carnivorous ones such as the tectibranch opisthobranchs, *Natica* and the muricacean *Stenoglossa* find their usual food in the bodies of other molluscs, lamellibranch or gastropod, all of which are provided with a shell into which they can withdraw and through which the predator must somehow make its way if it hopes to use the contents as food. Each of the groups mentioned above has solved this problem of gaining access to its food in a different way.

Such opisthobranchs as *Philine*, *Haminea* and *Scaphander* live on sandy or muddy bottoms in which there are often large numbers of small lamellibranchs, and it is upon these that the gastropods feed. They ingest the bivalves whole and pass them to a specialized portion of the oesophagus, the gizzard. Here there are developed calcareous plates linked by sheets of muscle to form a mill within which the shell of the prey is crushed and the flesh within exposed to the action of digestive juices secreted from the digestive gland (Fretter, 1937). This gizzard and the digestive gland are the two important parts of the gut in such animals and the stomach has lost the significance which belonged to it in many prosobranchs.

Natica likewise burrows into the sand at low water mark in search of bivalves upon which to feed, but this mollusc, perhaps because of the fact that it is itself enclosed within a rigid shell, is quite incapable of taking into its alimentary tract the whole body of its prey at once, as a tectibranch would do. Instead, it bores a hole through the shell and, with its radula, scrapes out the viscera of the lamellibranch. How this hole is bored was first described by Ankel (1937), who showed that on the under side of the tip of the snout in *Natica* lies a hemispherical boss covered with a richly glandular epithelium. The lamellibranch which is being attacked is wrapped round by the lobes of the foot of *Natica* and the gland pressed against the outer surface of its shell; a secretion of sulphuric acid takes place and an etching of the bivalve shell begun. It is almost impossible, so closely is the lamellibranch covered over

by the body of the gastropod, to see exactly what goes on during the process of boring, but sooner or later a hole is made through the shell, the proboscis of *Natica* is pushed through and the body of the prey gradually licked out.

Many of the stenoglossan prosobranchs are also able to attack shelled molluscs in a similar way. The Buccinacea, a group which includes the common British genera *Buccinum*, *Neptunea* (= *Fusus*) and *Nassarius* (= *Nassa*), are carrion feeders and do not bore; the Muricea, a group which includes *Ocenebra*, *Urosalpinx* and *Nucella* (= *Purpura*), do bore through the shells of gastropods and lamellibranchs or attack barnacles, though in this latter case they simply part the valves of the crustacean by means of their proboscis and do not make any hole through it. In the case of these gastropods the boring is done by mechanical and not by chemical means and it is possible with careful observation, to make out with considerable certainty what is actually happening during the process. The prey, usually a specimen of *Patella* or *Mytilus*, less commonly a *Littorina* or a bivalve, is embraced by the foot, the anterior corners of which are wrapped round the shell. A sucker, normally hidden in a depression on the anterior part of the sole of the foot (Fretter, 1946) is extruded, with the result that the prey is held under the proboscis of the whelk by foot and sucker in a fairly firm grip. Boring is begun by the extrusion of the odontophore from the mouth at the tip of the proboscis which has been everted sufficiently to bring it to rest on the surface of the shell of the prey. The radula rasps this with a series of short strokes all in the same direction, then there is a pause during which the odontophore is withdrawn, and when the rasping is begun again it is found that the odontophore has been twisted through an angle so that it now rasps the shell along a different line. This process is repeated over and over again with the hole deepening all the time. Should the gastropod be dislodged in the middle of the process and the gut opened it will be found to contain many minute chips of calcareous material embedded in a thick mucous material. This probably comes from the main salivary glands, but the muricean stenoglossans possess an extra pair of oral glands in the form of two tubes with thick muscular walls which open by a common pore placed mid-ventrally on the edge of the mouth. The cavity of each gland is lined by an epithelium containing two types of gland cell, one placed within the muscular layer and the other external to it and shedding its secretion to the lumen through ducts piercing the muscular coat. Precisely what part these glands play in the process of boring is not known, but that they are concerned in it appears a logical enough deduction from the position of their external aperture and their absence in the Buccinacea.

Once the hole has been bored in the shell the gastropod is still some way from consuming the body of the prey: it merely has access to it. A further adaptation, however, brings the food within reach—the possession of a long proboscis which can be insinuated through the hole so as to allow the radula to rasp the soft parts of the body of the prey, the rich gonad and digestive gland usually being attacked first. In the same way the Buccinacea use their proboscis to probe into the cracks and crevices within which the dead bodies of their prey are often to be found.

An interesting extension of this way of feeding leads to the ectoparasitic methods employed by members of the opisthobranch family Pyramidellidae (Fretter & Graham, 1949), each species of which seems to be confined in its attack to one particular species of host, usually a sedentary polychaet or mollusc, in conformity with the rule enunciated above that a carnivorous gastropod must attack prey even more slow-moving than itself. The pyramidellids lack a radula, but have the jaw in the roof of the buccal cavity transformed into a tubular tooth into which the salivary secretion is led. The mouth lies at the centre of a sucker at the apex of a long protrusible

proboscis and leads into a buccal cavity connected to a muscular suction pump worked by striated fibres. Pyramidellids tend to lurk in the immediate vicinity of the host upon which they feed, approaching it cautiously when about to do so. The proboscis is extended from some little distance away and is gradually and gently brought close to the surface of the body of the host, in some cases (*Chrysallida spiralis*), even being introduced into the gut through the mouth. A grip is obtained by means of the sucker and the body of the host pierced by the sudden projection of the tooth. In successful attacks this causes no more than a slight flinching on the part of the animal attacked and a rapid pumping carried out by the buccal pump of the pyramidellid sucks blood into its alimentary tract.

A limited number of other gastropods show converging trends towards parasitism: the eulimids and the styliferids creep amongst the spines of echinoids rasping at the animal's flesh and lead on to such total parasites as *Enteroxenos* and *Entoconchus*, which have become completely immobilized and dependent upon their hosts. Nevertheless, despite the apparent attractions which, it might be thought, the parasitic mode of life would offer to such slow-moving creatures as the molluscs that phylum remains on the whole one in which parasitic members are of rare occurrence.

REFERENCES.

- ANKEL, W. E. 1937. Wie bohrt *Natica*? *Biol. Zbl.*, **57**, 75-82.
 BOETTGER, C. R. 1930. Studien zur Physiologie der Nahrungsaufnahme festgewachsener Schnecken. Die Ernährung der Wurmschnecke *Vermetus*. *Biol. Zbl.*, **50**, 581-597.
 FORREST, J. E. 1950. The structure and function of the alimentary canal in dolid nudibranchiate Mollusca. *Ph.D. Thesis, University of London*.
 FRETTER, V. 1937. The structure and function of the alimentary canal of some tectibranch molluscs, with a note on excretion. *Trans. roy. Soc. Edinb.*, **59**, 599-646.
 ———. 1946. The pedal sucker and anal gland of some British Stenoglossa. *Proc. Malac. Soc.*, **27**, 126-130.
 FRETTER, V., & GRAHAM, A. 1949. The structure and mode of life of the Pyramidellidae, parasitic opisthobranchs. *J. Mar. biol. Ass.*, **28**, 493-532.
 GRAHAM, A. 1949. The molluscan stomach. *Trans. roy. Soc. Edinb.*, **61**, 737-778.
 PARKER, G. H. & VAN ALSTYNE, M. A. 1932. The control and discharge of nematocysts especially in *Metridium* and *Physalia*. *J. exp. Zool.*, **63**, 329-344.
 YONGE, C. M. 1928. Structure and function of the organs of feeding and digestion in the septibranchs, *Cuspidaria* and *Poromya*. *Phil. Trans. (B)*, **216**, 221-263.

THE TRANSFERENCE OF SPERM FROM MALE TO FEMALE PROSOBRANCH, WITH REFERENCE, ALSO, TO THE PYRAMIDELLIDS

By VERA FRETTER.

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(With 3 text-figures.)

In the majority of prosobranch gastropods the sexes are separate and reproduction concerns the coming together of male and female individuals; even in hermaphrodite forms cross fertilization is the rule. In the most primitive of the three orders of the sub-class, the Archaeogastropoda, which includes only marine species, external fertilization occurs: the male, in the vicinity of the female, sheds sperm into the sea, and so, apparently, stimulates the liberation of ova—such has been observed in *Haliotis* (Pelseneer, 1935), *Patina*, *Patelloida* (personal observation) and the trochids (Robert, 1902). The eggs are shed singly, their protective coats being a secretion either of the ovary or of the egg itself. The mesogastropods and the stenoglossa form egg capsules in the pallial region of the oviduct, a section of the duct which is not differentiated to any extent in the archaeogastropods:

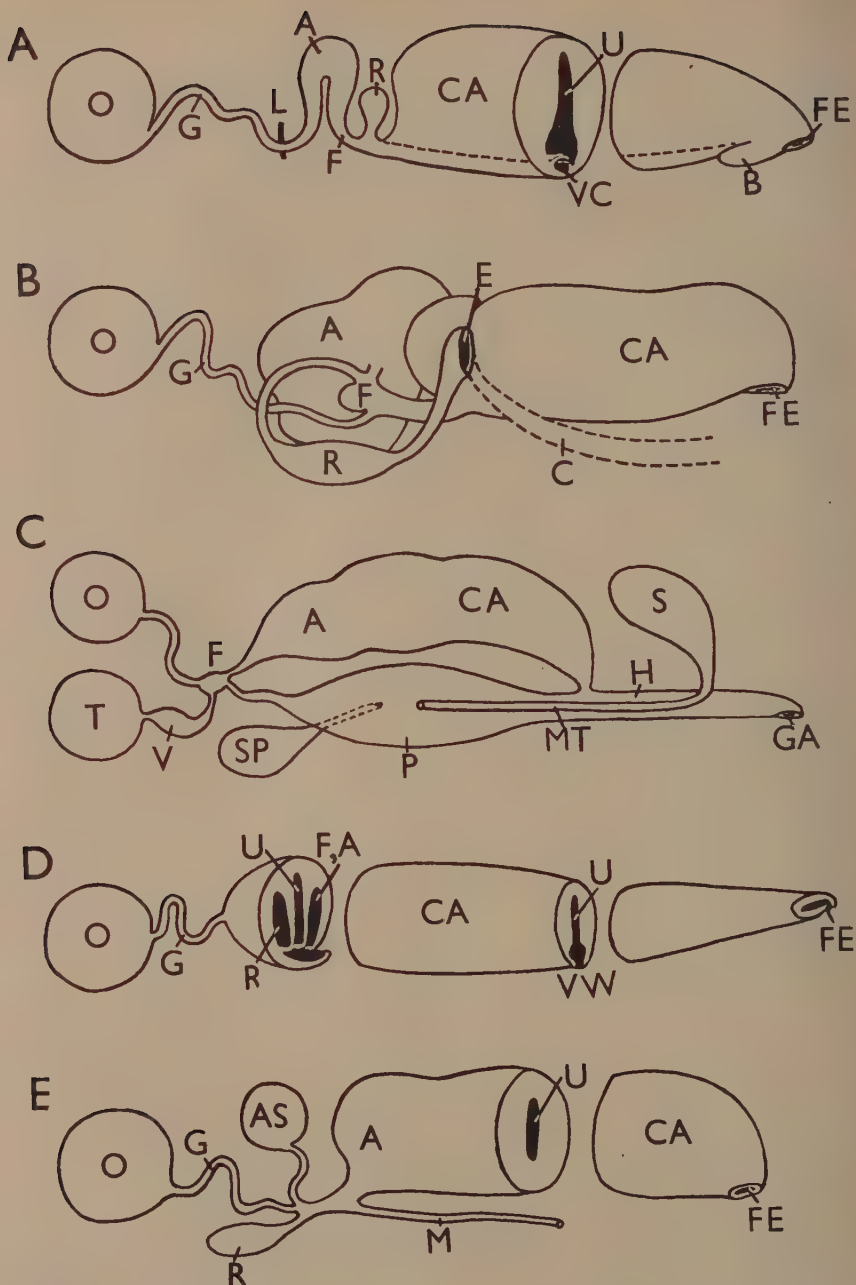


FIG. 1.—Comparative diagrams of the genital ducts of: A, *Nucella*; B, *Sheneopsis*; C, *Omalogyra*; D, *Turritella*; E, *Cingula fulgida*. The pallial duct is cut transversely in A to show the ventral sperm channel; D, to show the duct open to the mantle cavity; E, to show the absence of a ventral sperm channel. A, albumen gland; AS, accessory sac; B, bursa copulatrix; C, channel along outer surface of mantle; CA, capsule gland; E, entrance to receptaculum seminis;

here the eggs are embedded in albumen, and surrounded by a secretion which becomes less viscid and hardens when exposed to water. In such prosobranchs it is necessary for the ova to be fertilized before the secretions enclose them: they must meet the sperm in the upper part of the pallial duct. The sperm are usually deposited in the female by a penis, typically pedal in origin—as shown by its innervation—and arising from behind the right cephalic tentacle. When in use the penis is dilated with blood and may assume more than twice the size of its resting state; it is passed into the mantle cavity of the recipient and through the genital aperture. The mantle cavity, with a variety of functions to perform, must be sufficiently large to accommodate the distended penis and not be incommoded by its presence which may last up to half an hour, as in *Littorina saxatilis*, or three times as long, as in *L. obtusata* (Ankel, 1936). It is of interest to note that in the tectibranchs and nudibranchs, in which the mantle cavity is reduced, or has disappeared, copulating partners may be united for a much longer time: several hours or even days in *Aplysia* (Eales, 1921), and four or five days in *Archidoris britannica* (Pelseneer, 1935).

In the prosobranchs the pallial duct in both sexes traverses the length of the mantle cavity to near its mouth, and is typically closed off from that cavity; it presumably originated as a longitudinal pallial groove, though only in a few species is it represented by a morphologically open duct. In the male of *Littorina littorea*, though not in the female, it is open, and the gland cells which thicken its walls comprise the prostate. *Littorina* is one of the more primitive genera of the mesogastropods and the open vas deferens may represent a stage in the evolution of a closed pallial duct. The penis is provided with glands which open on wart-like protuberances on its surface, and, as suggested by Linke (1933), their secretion will help to maintain a hold in the mantle cavity of the female. In the female there is a pouch near the genital aperture, the bursa copulatrix, which receives the sperm and prostatic secretion; after copulation the sperm leave the bursa and make their way along a ventral channel of the pallial duct to the receptaculum seminis, which is distally placed (Linke, 1933). They orientate themselves in the receptaculum and await the discharge of ova from the ovary. In the stenoglossa (Fretter, 1941), such as *Nucella*, *Buccinum* and *Nassarius*, the oviduct has similar pouches (fig. 1A, B and R), connected by a ventral channel (VC) for dealing with the incoming spermatozoa.

There are exceptions to this usual method of transference of seminal fluid from male to female prosobranch, and these may be associated with a different type of penis, or the loss of a copulatory organ; they also involve changes in the structure of the pallial duct in both sexes.

In a number of genera the penis deposits sperm directly into the upper end of the pallial duct, either into a pouch, from which they are soon removed to the adjacent receptaculum, as in *Pomatias elegans* (Creek, 1951), or directly into the receptaculum, as in *Skeneopsis* (Fretter, 1948), *Capulus*, *Calyptreaea*, *Crepidula* (Giese, 1915), *Trivia* and *Lamellaria* (Fretter, 1946). In *Pomatias* and *Trivia* the mantle cavity is broad and the oviduct opens by way of a longitudinal slit in its ventral wall: this is a secondary opening which assists the expulsion of the large egg capsules and allows the penis to reach the upper end of the pallial duct. *Capulus*, *Calyptreaea*, *Crepidula* and *Lamellaria*—also with a broad mantle cavity—have a terminal genital aperture, and the

F, fertilization chamber; FE, female aperture; G, gonadial duct; GA, genital aperture; H, hermaphrodite duct; L, inner limit of mantle; M, muscular duct opening to mantle cavity; MT, muscular tube in lumen of vas deferens; O, ovary; P, prostate thickens walls of vas deferens; R, receptaculum seminis; S, muscular sac; SP, sperm sac in which unused sperm are digested; T, testis; U, lumen of capsule gland; V, vesicula seminalis; VC, ventral sperm channel; VW, ventral wall of capsule gland open to mantle cavity.

penis, passing through it, stretches the length of the pallial duct to the vicinity of the receptaculum. In *Skeneopsis planorbis* the method of copulation is unique. The penis is exceptionally long and, when in its resting position beneath the mantle skirt, its tip reaches the posterior end of the mantle cavity; it is slightly compressed laterally, and mucous glands opening along the dorsal and ventral walls lubricate the passage into the female. It does not enter the comparatively narrow mantle cavity of the female and make contact with the genital aperture, but is inserted between the mantle and the shell, on the right side of the body (fig. 1 B, C), passing to the upper end of the body whorl to deposit sperm in the duct of a receptaculum (R) which opens there (E).

Skeneopsis is an inhabitant of intertidal rock pools, though it is less confined to this habitat than another small prosobranch, *Omalogyra atomus*, the most minute of British molluscs, which has several specialized features in its reproductive system.

Omalogyra is hermaphrodite (Fretter, 1948) and during the summer months, when the *Ulva* on which it feeds is abundant, one generation follows the other very rapidly: in individuals collected at this time no structure which could act as a copulatory organ is developed; it is probable that self-fertilization is then practised. Only immature forms tide over the winter, the progeny of late summer or autumn spawners, and these develop slowly, coming to maturity in the spring. They differ from the summer forms in certain structural details. In the reproductive system the male organs are the first to mature, and through the lumen of the vas deferens (fig. 1 C, P) is a muscular tube (MT) with its open end directed posteriorly towards the vesicula seminalis (V), and its opposite end opening into a large sac (S) which arises from the anterior hermaphrodite portion of the pallial duct (H). "It is assumed that this is the copulatory organ: sperm liberated from the vesicula seminalis could be sucked through the penial tube into the muscular sac; the direction of the tube then being reversed so that it protrudes through the genital aperture (GA) and into the hermaphrodite duct of the copulating partner. The muscular wall of the sac would contract and so transfer the seminal fluid. The arrangement of these organs—a distensible sac associated with a muscular tube—is repeated in the Pyramidellidae in which copulation has been observed (Fretter & Graham, 1949).

The pyramidellids are parasitic opisthobranchs of small size, though, until recently, and solely on the basis of external features, they have been classified among the prosobranchs: they are typically monotocardian in appearance in that the visceral hump is large, wound into a dextral spiral, and enclosed in a stout calcareous shell into which the body can be completely withdrawn and sealed off by an operculum. The outstanding feature of the reproductive system is in the position of the invaginable penis: it lies in the haemocoel, apart from the rest of the genital organs, in a sheath which opens beneath the mentum and passes back through the nerve ring. This is a passage occupied in other molluscs only by the digestive tube and its intrinsic glands and muscles. Perhaps the penis was carried into this position by the elongation of the snout, in the development of the long, acrembolic proboscis which characterizes the pyramidellids; it remains associated with the genital aperture by a ciliated groove. During the copulation of *Odostomia* the individual acting as male creeps on to the dorsal surface of the shell of its partner. The penial tube is everted by pressure of the blood in the haemocoel, aided by muscles of the penial sheath, and, as a whip-like organ turgid with blood, is curved ventrally to reach the mantle cavity and enter the genital aperture of the second individual. Opening into the tube is a sac (fig. 2, SS) already filled with sperm from the vesicula seminalis, and its contents are now pumped into the hermaphrodite duct; they fill the receptaculum, surround its opening into the pallial duct, and are concentrated in the channel which connects this opening

with the genital aperture, and into which the penis is inserted. The pyramidelids have no bursa copulatrix. In *Odostomia* and *Chrysallida* the penis is a tube with blood spaces; in *Turbonilla* (Fretter, 1951 a) it is spoon-shaped (fig. 2, PE) with neither blood spaces nor glands, and in these two details resembles the penial tube of *Omalogyra*.

It has been suggested that the insertion of a penis into the mantle cavity of a prosobranch gastropod—which with two exceptions are aquatic—could interfere with the normal functioning of that cavity: through it passes a respiratory current of water carrying in the exhalant flow effluence from the kidney and the rectum. Some gastropods, microphagous feeders, make further use of this water stream by filtering from it particulate matter which comprises their food. *Turritella communis* feeds in this way (Graham, 1938). It is gregarious, frequenting muddy places, and to avoid clogging the gills with excess silt the mantle cavity is isolated from the environment by a curtain of branched tentacles, which surrounds the pallial opening. The pallial duct in *Turritella* is an open groove in both sexes (Fretter, 1946; Johansson, 1946), with glandular walls that form the prostate in the male and the capsule

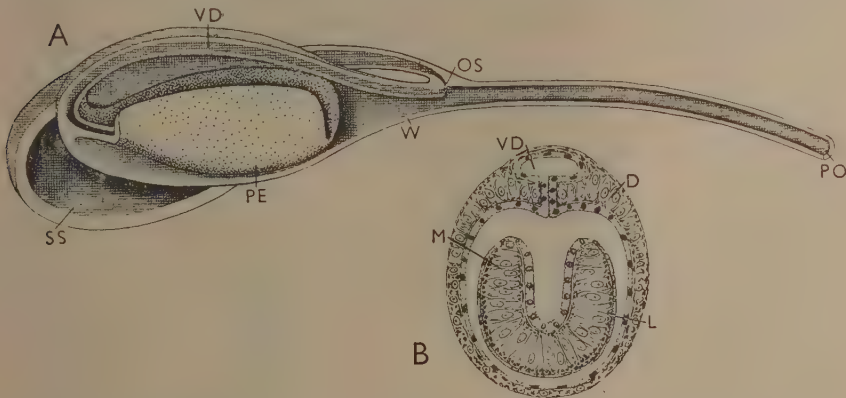


FIG. 2.—*Turbonilla elegantissima*. A, copulatory organs. The right wall of the sperm sac, the penial sheath, the vas deferens and of the posterior part of the penis has been removed. $\times 122$. B, Transverse section through penis and its sheath. $\times 271$. D, dilator muscles of penial sheath; L, longitudinal muscles of penis; M, muscles running between epithelia of penis; OS opening of sperm sac into penial sheath; PE, penis; PO, opening of penial sheath beneath mentum; SS, sperm sac; VD, vas deferens; W, wall of penial sheath.

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gland in the female (fig. 1, D). At its inner end the female groove is bordered by an open pouch on either side, one a receptaculum seminis (R), the other a fertilization chamber which is also the albumen gland (F, A). There is no penis in the male: these molluscs do not copulate. Should copulation be practised by the use of a penis in the normal position for a prosobranch, the isolation of the mantle cavity would be impaired in both male and female individuals. Since *Turritella* is gregarious, spawning of large numbers probably occurs simultaneously. Sperm embedded in prostatic fluid will, presumably, leave the mantle cavity of the male and be carried into the receptaculum of the female by the inhalant water current; the sperm are orientated in the receptaculum, their heads embedded in the epithelium. This open condition of the genital duct and the absence of a penis is almost certainly secondary and associated with the rigours of a ciliary food-collecting habit in a muddy situation.

There are other British mesogastropods in which the penis is lost and the pallial genital duct is open. These include *Cerithiopsis tubercularis* and *Triphora perversa* (Fretter, 1951) which are of small size, the shell rarely exceeding 8 mm. in length, and feed on silicious sponges; *Bittium reticulatum* (Johansson, 1947) of similar appearance, but herbivorous; and the larger carnivores *Clathrus clathrus* (Johansson, 1947) and *Balcis alba*. The helicoid spiral shell in these species is tightly coiled and has a small apical angle. The mantle cavity is narrow and deep, with a large gill towards the left side. In such a tight spiral there is considerable shortening of the right side of the body and so less space for the right half of the pallial complex—that is, the genital duct and rectum. It is therefore not surprising to find that the pallial genital duct in both sexes is narrow; never swollen with excessive development of glands; open throughout its course, the right and left walls as two glandular strips closely adpressed; and ends at some distance from the constricted

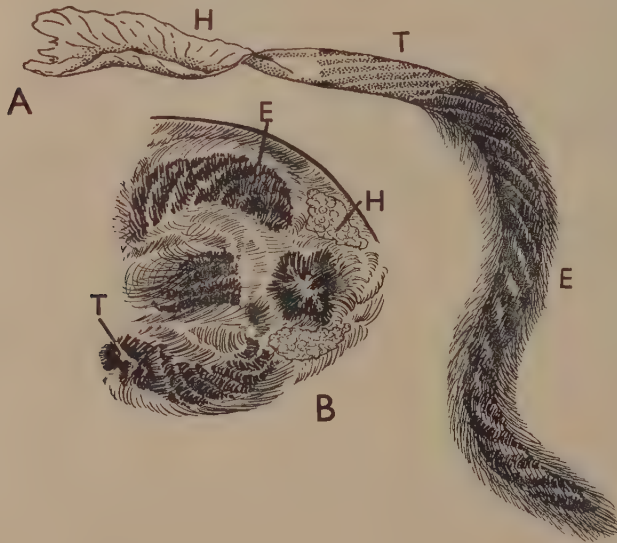


FIG. 3.—*Clathrus clathrus*. A, spermatozeugma; B, part of transverse section through the vesicula seminalis. ($\times$ about 134.) E, orientated eupyrene sperm; H, head of oligopyrene sperm; T, tail of oligopyrene sperm.

mouth of the shell. Perhaps in these prosobranchs the mantle cavity has reached a minimal breadth for maintaining a proper ventilation, and should it be still further restricted by a swelling genital duct, or the presence of a penis, its breadth might be brought below the limit for efficiency.

Prosobranch gastropods may have two types of spermatozoa: eupyrene sperm, the male gametes; and oligopyrene sperm which are of differing forms—they may be vermiform and motile, having eight to sixteen tails apiece in *Viviparus* (Hanson, Randall & Bayley, 1952), or they may be fusiform and with little power of movement as in *Nassarius* and *Fusus* (Pelseneer, 1935). It has been suggested (Hanson, Randall & Bayley, 1952) that the function of the atypical sperm is analogous to the seminal plasma of other animals, in that they provide nourishment for the eupyrene forms. In some gastropods they do more than this: they attain a relatively enormous size and each is the means of transport of thousands of male gametes which become orientated

in a regular order, their heads embedded in the cytoplasm of the nurse. In *Cerithiopsis tubercularis* this association takes place in the testis before either type of spermatozoon has attained its definitive proportions; in no part of the gonadial duct are the eupyrene sperm free. It is unusual to find orientated sperm in a vesicula seminalis (fig. 3 B). Ankel (1926) has described them in *Clathrus clathrus* arranged in longitudinal rows on the tails of the oligopyrene individuals (fig. 3 A)—such compound structures he terms spermatozeugmata. When these nurses are transferred to sea water they swim about vigorously dragging behind them their shimmering tails and covering greater distances than could, perhaps, be expected of the eupyrene form. For this they need their food reserves. Now both *Cerithiopsis* and *Clathrus* have an open pallial genital duct and no copulatory organs: it may be that the oligopyrene sperm obviate the possession of a penis by carrying their load to the upper end of the pallial duct to discharge it in the vicinity of the receptaculum seminis. In *Cerithiopsis*, however, no atypical sperm have been seen in the female; their ultimate fate is unknown. This is not so for the protandrous hermaphrodite *Janthina*, in which spermatozeugmata have been described in the male phase by Ankel (1930). In *Janthina* the genital duct is closed throughout its length; the mantle cavity is broad, and yet there is no penis. Graham (unpublished work) has found spermatozeugmata liberating eupyrene sperm in all parts of the genital duct in the female phase of *Janthina britannica*, even as far as the ovary, and he suggests that "the spermatozeugmata may swim from male to female, settling on the body of the latter and entering the genital tract", presumably by way of the genital aperture.

There is another prosobranch, dioecious and of small size, in which the pallial genital duct is closed and there is no penis—neither are there spermatozeugmata which might compensate its loss. This is *Cingula fulgida* which lives in rock pools: it differs in many structural details from other members of the genus, the differences being so great as to justify its removal from the class Rissoidea. In both male and female individuals the pallial genital duct is of considerable size, the walls are thickened by epithelial glands and the genital aperture is terminal, not far from the broad mouth of the mantle cavity. The glands in the male give copious prostatic secretion; in the female they provide albumen (fig. 1 E, A) and a fluid of conchiolin-like texture which forms the capsules (CA) for the eggs. The eggs are large, relatively few in number, and the young hatch in the crawling stage (Lebour, 1937). In the female system there is no bursa copulatrix, or ventral sperm channel along the oviduct; its plan is different from that of other gastropods—though it approaches that of *Theodoxus fluviatilis* (Fretter, 1946)—and we may suspect that modifications are correlated with the absence of a penis in the male. Running alongside the capsule gland, not far from its ventral wall, is a narrow muscular duct (M) which is shorter than the oviduct, so that it opens well within the mantle cavity. It communicates at the inner end with all parts of the reproductive system—the gonadial duct (G), pallial oviduct (A, CA), receptaculum seminis (R), and a large accessory sac (AS). During the breeding season, in spring and summer, the receptaculum contains orientated sperm, and in the accessory sac is a fluid which has the staining properties of prostatic secretion. Obviously there must be some means, which as yet can only be surmised, by which sperm are transferred from the male. The seminal fluid may be brought into the mantle cavity with the inhalant flow of water, and, from there, drawn up the accessory muscular duct which leads directly to the receptaculum. No prostatic fluid can be recognized in the receptaculum; it appears to be separated from the sperm and concentrated in the accessory sac. In *Theodoxus* there is a vaginal duct apart from the pallial duct, which may, as in the case of the muscular duct of *C. fulgida*, represent the ventral sperm channel of other prosobranchs. The reason for the absence of a penis in

C. fulgida is, so far, inexplicable—this species is only slightly larger than *Amalgyma*, and in both of these minute forms the transference of sperm is by an unusual method, which is, perhaps, correlated with small size.

Lastly, mention may be made of the rare mesogastropod *Adorthis* = *Tarvus subannulatus*. In his brief description of the reproductive system Woodward (1899) stated that the male has neither penis nor accessory gland, and that the vas deferens opens "high up and close to the external orifice of the kidney". The orifices, however, has a pallial section "which after running parallel to the rectum for a short distance opens into the mantle cavity". Unless *Adorthis* is an exception to all other mesogastropods which have been studied, internal fertilization occurs; yet we have no suggestion as to the way in which it is brought about.

These few examples illustrate the divers methods by which sperm are transferred from one prosobranch to another, and emphasize some of the relevant modifications in the genital duct and associated copulatory organs. Special reference has been made to the region of the duct connected with the mantle cavity, for it is influenced by the shape and size of that cavity, and the uses to which it is put. The pallial cavity, as stated by Graham (1948), "is probably the most essential characteristic of the Mollusca and has played an extremely important part in the evolution of the group: it is at one and the same time their strength, allowing them to live where other animals cannot, and their weakness, containing a collection of incompatible neighbours, which requires special treatment to avoid disaster".

REFERENCES.

- ANKEL, W. E. 1926. *Verh. Dtsch. Zool. Jahresvers.*, **31**.
 —. 1930. *Z. Zellforsch. mikr. Anat.*, **11**.
 —. 1936. *Prosobranchia* in: Grimpe, G. and Wagler, E., *Die Tierwelt der Nord- und Ostsee*, Teil 9b. Leipzig.
 CREEK, G. A. 1951. *Proc. zool. Soc. Lond.*, **121**.
 EALES, N. B. 1921. *Aplysia*. *L.M.B.C. Memoir*.
 FRETTER, V. 1941. *J. mar. Biol. Ass.*, **25**.
 —. 1946. *J. mar. Biol. Ass.*, **26**.
 —. 1948. *J. mar. Biol. Ass.*, **27**.
 —. 1951. *J. mar. Biol. Ass.*, **29**.
 —. 1951a. *J. mar. Biol. Ass.*, **30**.
 FRETTER, V. & GRAHAM, A. 1949. *J. mar. Biol. Ass.*, **28**.
 GIESE, M. 1945. *Z. zool. Zool.*, **114**.
 GRAHAM, A. 1938. *Proc. zool. Soc. Lond.*, **108**.
 —. 1948. *Form and function in the limnaea gastropod*. An inaugural lecture. Edinburgh College.
 HANSON, J. RANDALL, J. T. & BATLEY, S. I. 1952. *Exp. Cell. Res.* **3**.
 JOHANSSON, J. 1946. *Arch. Zool.* **38**.
 —. 1947. *Zool. Bidrag Uppsala* **25**.
 LEBOUR, M. V. 1937. *J. mar. Biol. Ass.*, **20**.
 LINKE, O. 1933. *Wiss. Meeresuntersuch.* (Abt. Helgoland), **19**, Heft 1.
 PILSENER, P. 1935. *Essai d'Ethologie Zoologique*. Brussels.
 ROBERT, A. 1902. *Arch. Zool. exp. gén.* (3), **10**.
 WOODWARD, M. F. 1899. *Proc. Malac. Soc. Lond.*, **3**.

ON THE FEEDING HABITS AND THE MORPHOLOGY AND MODE OF
FUNCTIONING OF THE ALIMENTARY CANAL IN SOME
LITTORAL DORID NUDIBRANCHIATE MOLLUSCA

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(With 5 text-figures.)

INTRODUCTION.

It is convenient to divide the nudibranchiate Mollusca into three main groups, the sacoglossans, the eolids and the dorids, although this should not be considered an all-embracing sub-division, for there are a few the sum of whose characters show that they fall into none of these sub-groups, but occupy an intermediate position.

The following account consists of a description of the feeding habits and the structure and mode of functioning of the alimentary canals of several littoral nudibranchs belonging to the dorid group.

In contrast to the dorids, the eolids, for the most part, feed on coelenterates and many of the peculiarities of their alimentary canals seem to be associated with the manipulation of food containing nematocysts (Graham, 1938). The dorids, on the other hand, have different foods and feeding habits. It has been known for long that many of them eat sponges and the statement has been made (Millott, 1937), with reference to one species, that digestion of the food is solely intra-cellular, that is that it takes place by the food particles being ingested by the digestive gland cells and digested inside them. It is obvious, however, that this cannot occur in *Archidivis pseudargus*, for example, for the sponge upon which this species feeds is taken into the buccal cavity in pieces averaging 2 mm. square, and many are bigger. And, further, its comparatively simple gut has no region set apart for triturating the food.

A. pseudargus is one of many dorids which are sponge feeders, but there are others which feed for the most part on ascidians and Polyzoa. The latter are almost always equipped with a modified radula and a suctorial apparatus at the anterior end of the alimentary canal which, by their coordinated action, serve to ingest the food which is generally in a semi-liquid form. The suctorial apparatus is the buccal pump, the functioning of which so far has escaped description.

In order to elucidate more fully the feeding habits and the structure and functioning of the dorid alimentary canal a series of thirteen British species has been investigated. The following pages contain an outline of this work.

THE SPONGE-EATING GLOSSODORIDIDAE.

A. pseudargus is a convenient example of a sponge-eating species. It may be found reasonably commonly near low-water mark on rocky shores close to, or often crawling on, the bread crumb sponge, *Halichondria panicea*, which is its food. In order to ingest and digest food of this kind certain modifications of the alimentary canal are required, for not only is a sponge which often forms a thin encrustation difficult to bite and convey into the mouth, but it also contains a mass of siliceous spicules which cannot be digested and must be removed from the gut. The proportion of indigestible residue in the food, therefore, is large and some mechanism is necessary for dealing with this.

The epithelium round the mouth and the lining of the buccal canal are glandular so that the food is well coated with mucus as soon as feeding begins and before it is taken into the alimentary canal. This serves as lubrication and also as a protection for the gut lining against the sharply pointed sponge spicules.

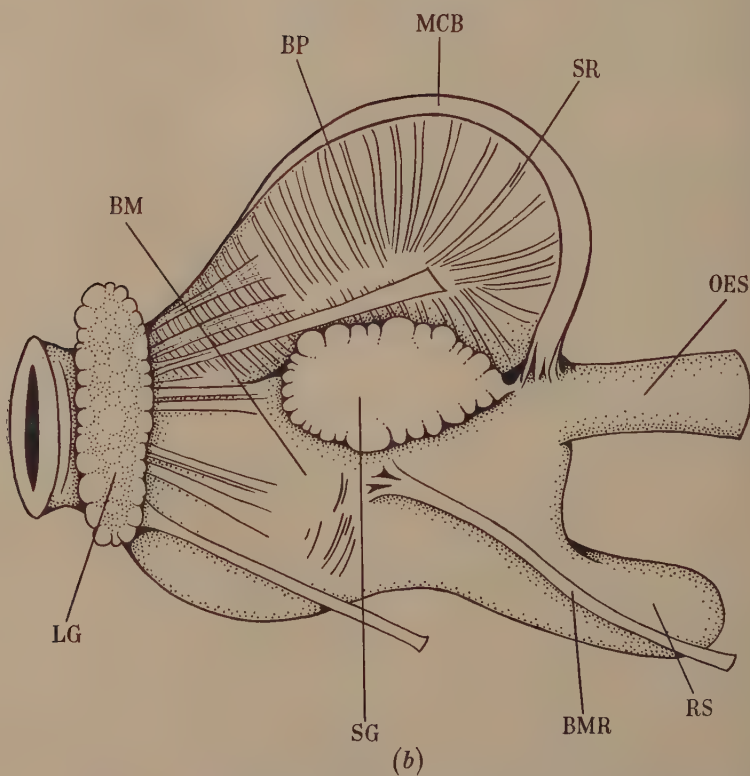
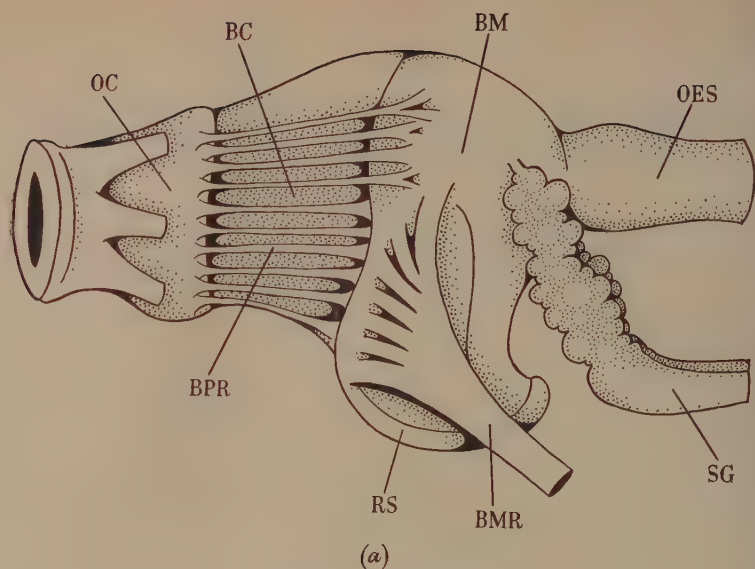


FIG. 1.—Buccal mass and associated structures of (a) *Archidoris pseudoargus* and (b) *Goniadoris nodosa* seen from the left side. Partly diagrammatic. (a) $\times 7$ approx. and (b) $\times 20$ approx. BC, buccal canal; BM, buccal mass; BMR, buccal mass retractor muscle; BP, buccal pump; BPR, buccal protractor muscle; LG, labial gland; MCB, median circular band; OC, oral canal; OES, oesophagus; RS, radular sac; SG, salivary gland; SR, superficial radial muscle.

Fig. 1(a) shows the structure of the anterior part of the alimentary canal in outline. There are no jaws. The radula is broad and bears numerous rows of many similar, hamate teeth (fig. 2(a)). The number of teeth in the fully formed radula may be as many as 5,000 to 6,000. In feeding, it is thrust through the mouth by the interplay of the odontophoral muscles and functions first as a rasp to break off pieces of sponge, and then as a scoop to convey them into the buccal cavity. Once there, the food is mixed with more mucus poured out by the glandular cells in the non-chitinized regions of the buccal wall and also with amylolytic and lipolytic enzymes secreted by the salivary glands. Digestion thus begins in the buccal cavity, but there is little breaking down of the food in this region of the gut, for, as feeding progresses, the food is passed rapidly through the buccal cavity along the oesophagus and into the stomach. Its passage is effected partly by peristalsis, for the gut wall is muscular, and partly by the pressure resulting from more and more food being taken into the buccal cavity, but cilia also help, more particularly to gather up the smaller fragments which become lodged in the grooves of the oesophagus, its wall being longitudinally ridged. A large amount of food is eaten at one meal, and when the animal stops feeding the stomach may be found to be distended by a great mass of sponge particles mixed with a bluish green liquid consisting of digestive enzymes and mucus.

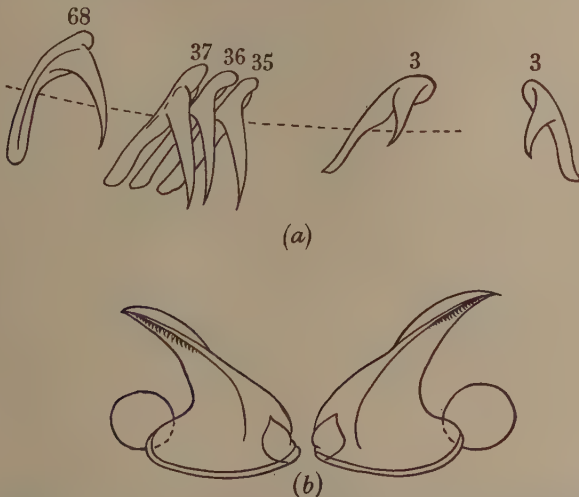


FIG. 2.—Radular teeth of (a) *Archidoris pseudoargus* and (b) *Goniadoris nodosa*. Both $\times 200$ approx. (a) shows the 3rd, 35th to 37th and 68th teeth of the left half of the 14th row from the front, and the 3rd tooth of the right half of the same row. This row contained 70 teeth on each side. (b) is the 14th row from the front.

In the stomach the food is subjected to a steady churning by the action of its muscular walls; cilia, however, also help in the thorough mixing of enzymes and food. Only a small proportion of the digestive enzymes present in the stomach has been secreted by the salivary glands, most of the enzymatic secretion found there having been elaborated in the digestive gland and passed by ciliary action from the digestive diverticula into the stomach. This secretory phase of the digestive cycle begins with the onset of feeding, and, providing some time has elapsed since the animal last fed, most of the digestive cells of the digestive gland will at this time be elaborating and secreting digestive enzymes which, at first, act extra-cellularly. Digestion is by now well under way and the larger pieces of food begin to break down. When digestion has reached a certain stage the spicules begin to fall free from the

sponge tissue and collect on the floor of the stomach where the majority of them are caught up by ciliary currents and passed into a blind caecum, the opening of which lies to the right of the oesophageal opening on the ventral wall of the stomach. The caecum lies beneath the stomach; in it the spicules are packed together into bundles by the action of cilia and coated with mucus preparatory to their passage through stomach and intestine as faecal pellets.

The food, now largely freed from sponge spicules and in a partly digested condition with its larger particles reduced to a conveniently small size, is passed from the stomach into the digestive ducts and diverticula. This is achieved partly by contractions of the stomach wall, but largely by the very strong ciliary tracts which line the ducts leading from stomach to digestive gland. In the digestive diverticula extra-cellular digestion continues, but also much of the partly digested food is ingested by the digestive cells, which now embark upon the second phase of their cycle, and digestion is completed intra-cellularly. The digestive cells are the only absorptive cells of the gut and, in addition to their digestive function, they also serve at this stage to absorb the products of extra-cellular digestion where this has been complete.

It is not surprising that the digestive gland is by far the largest organ in the body and occupies most of the haemocoel, for its size may be correlated with the fact that it secretes the greater proportion of the enzymes involved in digestion, that it alone is responsible for the absorption of digested food and that digestion is partly intra-cellular, all the food which is dealt with in this way having to be absorbed by its digestive cells. The digestive gland, therefore, is the site of great digestive activity, other parts of the gut, in particular the oesophagus and intestine, serving primarily for the conveyance of the food or its indigestible remains from one region of the alimentary canal to another.

Towards the end of the phase of ingestion and intra-cellular digestion the digestive cells change in appearance and are now to be found filled with the waste products of digestion and any indigestible material which may have been ingested earlier, such as small fragments of sponge spicules. A phase of egestion now ensues during which this waste matter is extruded by the digestive cells into the diverticula and conveyed thence, via the digestive gland ducts, to the stomach. This change in function is accompanied by a change in colour of the digestive gland tissue, for, in the secretory phase, the digestive epithelium is deep green or blue-green, and the digestive secretions liberated into the stomach are also blue-green in colour, but during the later phase of extrusion the colour of the digestive cells changes to brown or yellowish brown and the extruded material, which may be found filling the digestive gland ducts, is of the same hue. This latter function of the digestive cells has been described as excretion (Agersborg, 1923; Baba, 1937; Millott, 1937), and the digestive gland is then said to have a dual function, namely digestion and excretion, but it is probably best to reserve the term excretion for the process of nitrogenous excretion performed by the excretory organ and to call this phenomenon, which occurs in many molluscs, extrusion.

A complete account of the histological structure of the alimentary canal is beyond the scope of this paper, but, for an understanding of their proper functioning, some mention must be made of the detailed structure of the digestive diverticula. The digestive gland is made up of a vast number of diverticula leading into ducts which open eventually into the base of the stomach. The diverticula are arranged in lobes, although the gland itself does not present a clearly lobed appearance externally. The ducts from the lobes pass inwards towards the middle of the gland so that in a median cross section of it they may be seen clustered together at the centre. The epithelium lining the diverticula is ridged and bears three kinds of cells. These are shown in fig. 3. Commonest are the digestive cells which line the crest and sides of each ridge. They are, in turn, secretory, digestive and extrusive in function; during the digestive

cycle they pass through the series of phases which has already been described. In the troughs between ridges there are a few large secretory cells the function of which, I am led to believe, is the elaboration of digestive enzymes, and their secretion, in the form of droplets, may be found mixed with partly digested food in the lumen of the diverticulum. Having voided their secretion they present a collapsed appearance. At the sides of each trough and wedged in between the digestive and secretory cells are to be found smaller, columnar, undifferentiated cells which are not numerous and which form a reserve of digestive cells. It seems likely that they develop into digestive cells which they replace as need be, although this is not easy to confirm.



FIG. 3.—*Archidoris pseudoargus*. Epithelium of digestive diverticulum, phase of secretion. $\times 450$ approx. A, amoebocyte; BM, basement membrane; CTM, connective tissue and muscle; C3, third type of cell; DC, digestive cells; UC, undifferentiated cell.

The concluding stages of the digestive cycle are concerned with the removal from the gut of sponge spicules and other indigestible remains and waste products of digestion. The regions of the alimentary canal concerned with this are the stomach, caecum and intestine. The bulk of the sponge spicules, separated from the food in the stomach during extra-cellular digestion, are conveyed by ciliary action into the caecum, there to be moulded into compact faecal pellets. Those which do not succeed in reaching the caecum, for it would seem that there are far more spicules than can be dealt with by it, are conveyed by a strong ciliary tract on the dorsal wall of the stomach to the intestinal opening and in the intestine are mixed with mucus and moulded into faecal rods. The caecum is a muscular sac, and by its periodic contractions faecal pellets are forced from it into the base of the stomach, there to be caught up by ciliary currents and conveyed dorsally to the opening of the intestine. This action of

the caecum can be seen readily in a specimen dissected alive at the appropriate time. Examination of serial sections cut at this stage in the digestive cycle has further shown that a number of faecal pellets may be expelled from the caecum in quick succession. Removal of spicules takes place whilst the digestible portion of the food is in the digestive diverticula, or is being dealt with intracellularly. Later in the cycle, waste material, extruded from the digestive cells, passes from the digestive gland ducts in the form of a brown or yellowish brown mass into the stomach where, too, it may enter the caecum or pass directly to the intestinal opening. The phases of the digestive cycle are not clearly separated one from the other and some overlapping occurs, so that it is not uncommon to find that the caecum contains a mixture of sponge spicules and extrusion matter from the digestive cells.

The histological structure of the caecum is complex and the appearance of its epithelium varies according to the digestive activities of the animal. A point of considerable interest is that the evidence seems to show that between meals, and when the caecum is not engaged in faecal elaboration, it may have an excretory function, but a discussion of this is not entered into here. A dual function of the caecum has been described recently in *Jorunna* (Millott, 1937), and, much earlier, Eliot (1910) showed that he had observed the caecum of *A. pseudoargus* in the excretory phase, but he was unable to suggest a correct functional interpretation of what he saw. It is clear that an examination of the caecum at any single stage in the cycle of its activities can give little indication of the full range of its functions.

The intestine is a long, narrow tube of even bore and calls for little comment. Its ridged walls are ciliated and glandular (fig. 4) and its function is to complete the moulding of the faecal pellets which leave the anus as compact but friable rods easily conveyed by ciliary action outside the peri-anal circle of gills.

Mucus plays an important part in the functioning of the alimentary canal. Secreted by epithelial and sub-epithelial glands, it is poured onto the food when feeding begins and during its passage through the oral canal to the buccal cavity. A further copious secretion of it occurs in the oesophagus, but the stomach is non-glandular, since it serves as a muscular receptacle for extra-cellular digestion and as a region where the food is well churned and thoroughly mixed with the digestive enzymes. In contrast to it, the caecum, digestive gland ducts and intestine are all glandular. The mucus serves as a lubricant, essential for the proper functioning of cilia, easing the passage of the food through the alimentary canal, but it also gives protection to the gut epithelia which are liable to penetration by sponge spicules or sharp fragments of them.

From the foregoing description it will be appreciated that the alimentary canal of *A. pseudoargus* is comparatively simple in form, but has certain noteworthy features, salient amongst which are the absence of jaws, the many-toothed, rasping radula, the lack of a triturating mechanism, the caecum for faecal pellet formation and the relatively enormous digestive gland. These structural peculiarities may be correlated with the physiology of the gut, particularly with the fact that digestion is initiated extra-cellularly and that the complete cycle is a combination of extra-cellular and intra-cellular digestion. Also of importance is the copious secretion of mucus during feeding and digestion in all regions except the stomach and certain chitinized areas of the buccal cavity. The significance of a higher pH in the intestine than in other regions of the alimentary canal is probably that it controls the viscosity of the intestinal mucus and therefore the solidity of the faecal pellets.

Many dorids besides *A. pseudoargus* subsist on a diet of sponge. Thus, to mention only two others, *A. stelleri* has a preference for *Stylotella columella*, and the brick-red *Rostanga rufescens* eats *Microciona atrasanguinea*. The form and method of functioning of the alimentary canals of these species have not been found to differ in any fundamental respects from *A. pseudoargus*.



FIG. 4.—*Archidoris pseudoargus*. Photomicrograph of a transverse section of the intestine. Stained iron haematoxylin and mucicarmine. $\times 65$ approx. CGE, ciliated and glandular epithelium; MCT, muscle and connective tissue; SEG, sub-epithelial glands.

GONIODORIS AND OTHER SUCTION FEEDERS.

Many of the smaller dorids, such as *Acanthodoris*, *Goniodoris* or *Onchidoris*, differ in their feeding habits from *A. pseudoargus* and its allies in that they do not eat sponges. It is on record that they may take a variety of foods, both plant and animal, but it is certain that ascidians and polyzoans form the staple diets of a number of species. Correlated with the different type of food, the structure of the alimentary canal and the mechanism of feeding in these dorids differ in certain fundamental respects from those of the Glossodorididae. They are essentially suction feeders. It is not surprising, therefore, to find that the smaller dorids occupy a different niche on the shore as compared with the sponge-eating species. Their ideal habitat is near low water mark, or in the deeper rock pools, under rocks and stones where Polyzoa, compound ascidians and other encrusting forms abound.

The two British species of *Goniodoris* are good examples of this group. *G. nodosa* and *G. castanea* feed chiefly on *Dendrodoa* and *Botryllus*. In feeding, the hard parts of the food, i.e. the ascidian test, are not ingested, but the contents of the prey are sucked out, thus necessitating a modification of the anterior part of the alimentary canal. There are no jaws. In both species the radula is small and contains few teeth; the 88 in *G. nodosa* are arranged in 22 rows of 4 teeth each, there being no central tooth. The teeth are not all alike, the inner pair in

each row is large, curved and pointed, with denticulate inner edges, whereas the outer ones are much smaller and plate-like (fig. 2(b)). The larger teeth cut into the food, and, once penetrated, the contents are sucked out by the action of the buccal pump, a highly muscular, bulb-like structure on the dorsal surface of the buccal mass (fig. 1(b)). The actions of the radula and the buccal pump are coordinated in such a way that when the buccal pump is sucking (i.e. its walls expanding), the mouth is open and food is drawn into the buccal cavity, and, perhaps, into the pump itself; when pumping, the mouth is closed and the contents of the pump and the buccal cavity are forced along the oesophagus to the stomach. Unlike the condition in *A. pseudoargus*, therefore, where the passage of food from the buccal cavity to the stomach is effected principally by ciliary and muscular means, in *Goniodoris* the non-particulate food is pumped along the oesophagus, although cilia, and, to

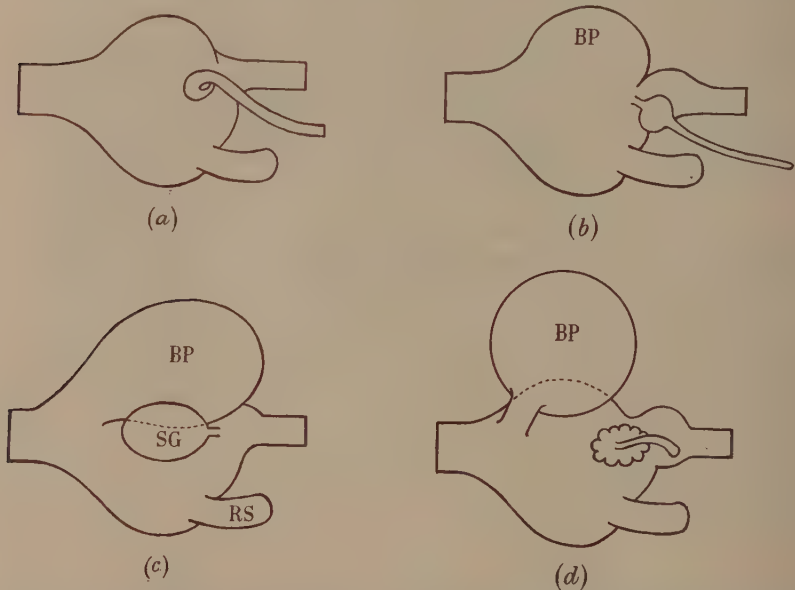


FIG. 5.—Diagrammatic representation of the buccal mass and associated structures seen from the left side in (a) *Palio nothus*, (b) *Acanthodoris pilosa*, (c) *Goniodoris nodosa* and (d) *Onchidoris fusca*. Not drawn to scale. BP, buccal pump; RS, radular sac; SG, salivary gland.

a lesser extent, peristalsis play some part in this. The movements of the buccal pump are fairly rapid, and therefore the opening and shutting of the mouth and the action of the radula are also rapid. Occasionally, in *G. nodosa*, where the dorsal integument is sufficiently transparent, the movements of the buccal pump may be seen through the body wall.

Much of the interest of the gut centres round the buccal mass.

The buccal pump is a unique and complex structure and calls for further comment. Its degree of development differs in different genera and species of this group of the dorids so that a series can be traced leading from a less to a more specialized condition (fig. 5). In *Palio nothus* (a member of the Limaciidae and not a true suction feeder) the dorsal wall of the buccal mass is expanded to form a slight muscular protuberance suggesting an early stage in the formation of a buccal pump. In *Acanthodoris pilosa* the buccal pump, although well developed, is not distinct from the buccal mass and opens into the buccal cavity anteriorly

by an elongate slit so that it has no stalk or pedicel. The next stage is to be found in the two species of *Goniodoris* in which the connection between pump and buccal cavity takes the form of a short, but relatively stout pedicel, whilst the extreme development occurs in dorids such as *Adalaria proxima* and *Onchidoris fusca*, where the pedicel is narrow and slender and where the buccal pump itself is a compact, pea-shaped, highly muscular organ sometimes lying to one side of the mid-dorsal line of the buccal mass. These are examples chosen at random and from several families and this is not to be regarded as a phylogenetic series, for in a single family, for example the Onchidorididae, the buccal pump may show different degrees of development in different species. Its degree of development can be correlated with the nature of the food and the animal's feeding habits.

The greater part of the wall of the buccal pump is composed of large muscle cells, the deep radials or dilators, arranged radially with respect to the central cavity. Measurements from fixed and sectioned material show that these cells may be as much as $500\ \mu$ long and $50\ \mu$ wide, although they vary greatly in size. On its surface, and sandwiched in between the outer ends of the deep radials, are small groups of superficial radial muscles fanning out from the centre of each side of the buccal pump (fig. 1(b)). The muscular complement of the wall is completed by a median circular band that encircles the pump in a vertical plane. The central cavity is a narrow slit lined by chitin secreted by an epithelium of columnar cells.

In functioning, the buccal pump performs a cycle of events brought about by the interplay of the muscles of its walls. The chief function of the deep radials is to confer rigidity on the lateral walls, which is essential for the proper functioning of the other muscles. This is at a maximum when they contract at the beginning of the cycle. The contraction of the median circular band, which follows, increases the volume of the central cavity and constitutes the suction phase of the cycle. By this means food is drawn through the mouth into the buccal cavity, and, to a lesser extent, into the pump itself, although food is rarely found in it even in a specimen dissected immediately after feeding. In the second half of the cycle, when the median circular band and to some extent also the deep radials are relaxed, contraction of the superficial radials decreases the volume of the central cavity and pumps the food farther back into the buccal cavity and into the oesophagus. The contraction of the superficial radials is a weaker action than that of the median circular band and this prevents the food being forced through the mouth which is shut at this time.

Eliot (1910) remarked upon the presence of a buccal pump (he called it the *ingluvies buccalis*) in a wide range of smaller dorids, but stated that he had never succeeded in discovering how it functioned, although he recognized that the radula was not masticatory in function, but served primarily as an organ of penetration. The foregoing description, although brief and simplified and based upon the condition of the buccal pump in *Goniodoris nodosa*, doubtless serves to show how this organ functions in most species which possess it.

The structure and physiology of the remainder of the alimentary canal require only brief description.

Salivary glands are present in both species of *Goniodoris*. Much reduced, however, they are small and lobed in *G. nodosa*, minute and spherical in *G. castanea*, and, lying at the sides of the buccal mass, have short ducts to the buccal cavity. The salivary epithelium contains glandular and ciliated cells. The oesophagus is a straight tube connecting buccal mass with stomach and is remarkable in having a ciliated, but non-glandular epithelium, thus modified for dealing with semi-liquid, largely non-particulate food.

In the typical dorid fashion the stomach, partly buried in the digestive gland, is divided into ventral and dorsal regions which are distinct not only topographically, but also histologically. The ventral stomach is a thin-walled sac, whilst the walls of the dorsal stomach are thicker and more muscular. In

G. nodosa both regions bear a ciliated epithelium for the most part, but in the dorsal stomach, close to the intestinal opening, this is interrupted by a restricted area of the wall which is chitinized, a development which is much more marked and extensive in *G. castanea*. In this species also the ventral stomach is ciliated, but the whole of the dorsal stomach has a chitinized lining thrown into a series of 18 to 20 prominent, longitudinal ridges bearing deep chitin at their apices, so that when the stomach contracts the lumen tends to be occluded. The reason for this development of chitin is not clear, but a possible function of the mechanism is to triturate any solid particles in the food which may have reached this part of the alimentary canal as described in *Hancockia californica* (MacFarland, 1923) and *Melibe leonina* (Agersborg, 1923), or, alternatively, it may function as a sieve or filter designed to prevent the contents of the ventral stomach passing into the intestine until digestion is complete.

There is no caecum and this is yet another feature to be correlated with the animal's diet, for the food contains little or no particulate matter which would require to be moulded into compact faecal rods like the spicules of *Halichondria*.

In general the relationships of the stomach to digestive gland are as in *A. pseudoargus*, ciliated and glandular ducts leading from one to the other.

No experimental evidence is available concerning the method of digestion of the food in *Goniodoris*, but, judging from the histology of the digestive gland, which in both species contains secretory and digestive cells, it seems likely that the food, pumped and swept into the stomach, there passes through the initial stages of digestion extra-cellularly later to be ingested in the digestive diverticula where the process is completed intra-cellularly. No fewer than four different types of cells line the digestive diverticula—digestive cells, interstitial cells and two kinds of secretory cells. Of these, the digestive cells are most numerous and, as in *A. pseudoargus*, they pass through a cycle of phases during the digestion of a meal. The waste products of digestion, extruded from the digestive cells, and any indigestible material are passed from the digestive diverticula into the stomach and thence to the intestine. Slight morphological and histological differences distinguish the intestine of *G. castanea* from that of *G. nodosa*. In the former there is a well-developed typhlosole and the epithelium is ciliated and glandular, whereas in the latter a small typhlosole occurs in the first part of the intestine, but does not persist, and the ciliated epithelium is devoid of glandular cells. The faeces, usually orange or orange-brown in colour, undergo but little moulding during their passage through the intestine and issue from the anus in small masses which readily break up, and are quickly carried away from the circlet of gills by ciliary action.

Taking food which is nearly liquid and in which particulate matter is reduced to a minimum has resulted in a simplification of the gut in certain respects, notably in the disappearance of the caecum and in either the absence of mucous glands or a great reduction in their number.

In all the dorids which have been considered the alimentary canal is built on essentially the same plan and the principal modifications which occur concern the structure of the buccal mass, the presence or absence of a caecum and the details of the histology of the digestive gland. This basic similarity is to be expected in animals which are closely related, for the dorids form a compact phylogenetic group, and have the same general habits. The modifications which have been described above result from the adoption by different families of different feeding habits and it is not surprising to find that the choice of different types of food has resulted in the evolution of differing means of its ingestion. Once within the alimentary canal, however, it is dealt with in essentially the same way in all.

AMOEBOCYTES.

No account of the process of digestion in the dorid nudibranchs would be complete without some mention of amoebocytes. A full description of them is

beyond the scope of this paper, but there is no doubt that they play a conspicuous and important part in the digestive cycle, and this is borne out by experimental evidence. Probably not all of the same kind, they cluster round the food as it enters the stomach and are to be found in large numbers in different regions of the alimentary canal during the digestion of a meal.

SUMMARY.

(1) The alimentary canal throughout the dorids is basically similar in structure and physiology, but different feeding habits result in certain modifications.

(2) *Archidoris pseudoargus* is a sponge-eating species which feeds on *Hali-chondria panicea*. The form and mode of functioning of its alimentary canal are described and compared with those in others of similar feeding habits. Food is ingested by means of the broad, many-toothed radula which acts like a rasp and a scoop. Copious secretions of mucus give protection to the gut and act as a lubricant. Digestion is at first extra-cellular, but is completed intra-cellularly. A caecum, opening from the stomach, has the principal function of compacting the sponge spicules into faecal rods, but possibly it also has an excretory rôle. The digestive gland epithelium bears three kinds of cells, of which the digestive cells are commonest.

(3) *Goniodoris nodosa* and *G. castanea* are suction feeders that eat ascidians. Like many of the smaller dorids they possess a buccal pump, which, acting in conjunction with the cutting radula, serves to ingest the semi-liquid food. The absence of particulate matter in the food is reflected in a simplification of the gut, notably in the absence of a caecum and a reduction in the secretion of mucus.

(4) Amoebocytes play an important part in digestion.

The nomenclature adopted is that recently revised by Winckworth (personal communication, March 1949).

A detailed account of the investigation described in the foregoing pages is being prepared for publication.

REFERENCES TO LITERATURE.

- AGERSBORG, H. P. K. 1923. The Morphology of the Nudibranchiate Mollusc *Melibe* (syn. *Chironaera*) *leonina* (Gould). *Quart. J. micr. Sci.*, **67**, 507-592.
- BABA, K. 1937. Contribution to the Knowledge of a Nudibranch, *Okadaia elegans* Baba. *Jap. J. Zool.*, **7**, 147-190.
- ELIOT, C. 1910. *A Monograph of the British Nudibranchiate Mollusca*. Part 8 (suppl.), London, Ray Society.
- GRAHAM, A. 1938. The Structure and Function of the Alimentary Canal of Aeolid Molluscs, with a Discussion on their Nematocysts. *Trans. roy. Soc. Edinb.*, **59**, 267-307.
- MACFARLAND, F. M. 1923. The Morphology of the Nudibranch Genus *Hancockia*. *J. Morph.*, **38**, 65-92.
- MILLOTT, N. 1937. On the Morphology of the Alimentary Canal, Process of Feeding, and Physiology of Digestion of the Nudibranch Mollusc *Jorunna tomentosa* (Cuvier). *Phil. Trans. (B)*, **228**, 173-217.

THE CHROMATOPHORE SYSTEM OF CEPHALOPODS

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(With Plates 1 and 2, and 1 text-figure.)

A. INTRODUCTION.

One of the difficulties in studying the organization of behaviour, is that we have few ways of systematically collecting data which could be used to express the differences in organization of the neuropils of brains of the same

and different species. I want to try to illustrate this difficulty by reporting one aspect of the work which Professor J. Z. Young and I have been doing during the past five years. Some of this work has already been described, Boycott & Young (1950) and Young (1951), (see also Sanders & Young, 1940).

B. THE CHROMATOPHORE SYSTEM OF CEPHALOPODS.

The chromatophore system and chromatic behaviour of cephalopods is already known in some detail and good reviews by Parker (1948) and Sereni (1930) are available. I shall not occupy myself with discussing the differences between their conclusions and ours, since detailed papers on most of the data mentioned are in preparation.

1. *The chromatophores.*

The chromatophores of cephalopods are small bags of coloured material lying in the skin. They are expanded by the contraction of radially arranged muscle fibres. The elasticity of the chromatophore wall contracts the colour cell when these muscle fibres relax. In its expanded state the diameter of a chromatophore may vary from twice to sixty times its diameter when contracted. There are from four to twenty-four muscle fibres per chromatophore. The nerve cell bodies of the fibres innervating the chromatophore muscles are within the central nervous system. The fibres of these cell bodies run, without synapse in the stellate ganglion, directly to the chromatophore muscles (Sereni & Young, 1932).

2. *Patterns of colour change in cephalopods.*

The patterns of chromatophore activity of *Sepia officinalis* L. have been described by Holmes (1940). There is a wide range of complicated patterns produced by the differential expansion and contraction of the three types of chromatophore (red, brown and orange). While there are variations of density of chromatophores on the different surfaces of the body, the types of chromatophore on any one surface are evenly distributed. The patterns of colour are, therefore, direct representations on the surface of the animal's body of central neural events. *Octopus vulgaris* Lamarck also produces complicated patterns, many of which are directly comparable to those of *Sepia*.

Loligo vulgaris Lamarck appears to be unable to produce complicated patterns of colour. The animal is either a pallid white when swimming freely and undisturbed, or a uniform red-brown colour when disturbed, being then darker dorsally than ventrally.* The only living *Argonauta argo* L. that I have been able to observe showed a similar simplicity of chromatic behaviour.

We can therefore contrast the complexity of the patterns of *Sepia* and *Octopus* with the simplicity of colour changes in *Loligo* and *Argonauta* and enquire into the differences in neural arrangement of the chromatophore system of the four animals.

3. *The chromatophore system of Octopus vulgaris.*

The cell bodies of the fibres innervating the chromatophore muscles of *Octopus* are concentrated into four lobes situated in the suboesophageal ganglia. Two *posterior chromatophore lobes*, innervating the chromatophores of the visceral mass, lie in the palliovisceral ganglion. Two *anterior chromatophore*

* It is worth noting that Stevenson's (1934) account of *Loligo pealii* Lesueur suggests a more complex chromatic behaviour than I have yet observed in *Loligo vulgaris*. Judging from his account the patterns are simpler than in *Sepia* and *Octopus* and therefore my thesis is not affected. Indeed a comparison of *L. vulgaris* and *L. pealii* might provide additional experimental material. I have used *L. pealii* in fig. 4, Pl. 2, since the brain of *L. vulgaris* is not yet available for photography.

lobes, innervating the chromatophores of the head and arms, lie in the pedal ganglion. There are transverse commissures between the two anterior and the two posterior chromatophore lobes. Each lobe innervates only the chromatophores of its own side. These lobes are the final common pathways of the chromatophore system and are therefore classified as lower motor centres (Boycott & Young, 1950). The higher motor part of the chromatophore system lies above the oesophagus. It consists of a pair of small lobes, the *lateral basal lobes*, which bulge out from the lower side of the posterior wall of the supra-oesophageal mass. Each lateral basal lobe sends a tract to the anterior and one to the posterior chromatophore lobe of its own side. These tracts can be shown by degeneration experiments to be efferent. In addition there are interchromatophore connectives between the anterior and posterior chromatophore lobes of each side. Along these connectives fibres run between ipsilateral suboesophageal chromatophore lobes, and the posterior chromatophore tract of the lateral basal lobe sends some of its fibres through this connective to the anterior chromatophore lobe. The connections are summarized in text-fig. 1.

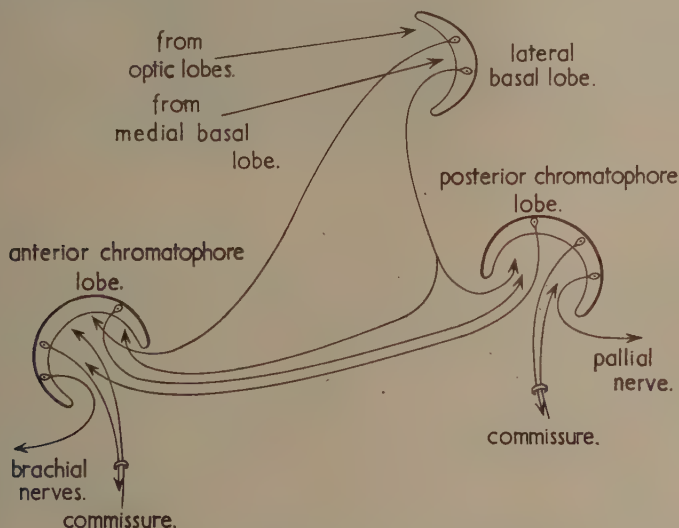


FIG. 1.—Diagram of the chief connections of the chromatophore lobes of *Octopus vulgaris*.

This system can be excited by fibres coming from optic, tactile and static sense organs. These afferent fibres probably work through the lateral basal lobe, although some tactile fibres may go direct to the suboesophageal chromatophore lobes. It is probable also that another supraoesophageal lobe, the *medial basal lobe*, enters into the system. The detailed relationships of this region are still obscure.

4. The chromatophore system of *Sepia*, *Loligo* and *Argonauta*.

The gross arrangement of the chromatophore system of *Sepia*, *Loligo* and *Argonauta* is the same as for *Octopus*.* Probably correlated with the differences

* Apart from those mentioned there are many other differences of detail, e.g. in the interchromatophore connectives and the way in which the lateral basal lobe tracts enter the chromatophore lobes. It has not therefore been possible to provide exactly comparable photographs.

in complexity of the patterns of colour change there are differences in the development of the lobes. In *Loligo* and *Argonauta* the posterior chromatophore lobe appears to be relatively smaller than in *Sepia* and *Octopus*. *Loligo* with its simple patterns does not have a clearly delineated anterior chromatophore lobe, although a corresponding area of cells can be recognized. In *Argonauta* and in *Sepia*, the anterior chromatophore lobe is not so clearly marked off from the pedal ganglion as in *Octopus*. A possible factor contributing to the small size of the anterior chromatophore lobe in *Sepia* and *Loligo* is the relative shortness of the arms compared with *Octopus*. There are thus presumably fewer chromatophores to be innervated. But I do not want to labour these points; more suggestive comparisons can be made from a consideration of the posterior chromatophore lobes.

5. The posterior chromatophore lobes.

The posterior chromatophore lobes of the four animals show considerable variations (figs. 1, 2, 3, 4, Pls. 1 and 2). We shall not concern ourselves with the wide variations in cell size and thickness of cell wall, for they are difficult to evaluate without a detailed knowledge of the relative sizes of the animals.

The processes of the cell bodies that form the cell wall stain only faintly, but they can be seen running through the neuropil and out into the pallial nerve, the interchromatophore connective, or the commissure. Presumably some of the processes, probably those of the smaller cells, remain within the lobes as 'association' fibres. In their passage from the lobe the efferent fibres pass through a network of darkly staining fibres more or less regularly arranged. Probably most of the darkly staining fibres, in the case of *Octopus*, are afferent to the lobe, coming from the lateral basal lobes as well as from the other chromatophore lobes and including, perhaps, tactile fibres from the periphery.

In *Octopus* these darkly staining afferent fibres are arranged in a regular lattice-work of criss-crossing bundles (fig. 1, Pl. 1). When the lateral basal lobe is removed degeneration granules appear in this network. Strands of this network are drawn out into pockets between the cells of the cell layer. These pockets of fibres branch and single nerve fibres can be found running in and out amongst the cell bodies, especially at the periphery of the lobe. The cell walls of *Sepia*, *Loligo* and *Argonauta* appear not to have these pockets of fibres, or fibres running in between the perikarya.

In *Sepia* an equally regular arrangement of the neuropil is seen (fig. 2, Pl. 1). It has been possible to trace the course of the tract from the lateral basal lobe through the neuropil of the posterior chromatophore lobe. The tract enters the anterior lower face of the lobe and its fibres pass across the efferent fibres of the lobe, sending off collaterals as they do so. Towards the hinder end of the lobe a bundle of fibres separates and crosses to the opposite chromatophore lobe in the commissure of the posterior chromatophore lobes. These fibres then run through the neuropil across the efferent fibres in the reverse direction to the fibres of the lateral basal lobe tract entering the chromatophore lobe of this side. The efferent fibres leaving these two lobes are thus influenced by afferent fibres from the ipsilateral and contralateral lateral basal lobe.

In *Loligo* and *Argonauta* (figs. 4, 3, Pl. 2) such regular arrangements are not apparent. Both these animals have afferent and efferent components, directly comparable with *Sepia* and *Octopus*, but the neuropil is a tangled mass of fibres presenting no very regular and therefore no very obvious organization.

These descriptions are incomplete and uneven. They have been based only on brains stained with a modification of Ramon y Cajal's block silver technique, supplemented in the case of *Octopus* and *Sepia* with Golgi-Cox staining. I have not given, and indeed am as yet unable to give, details of the

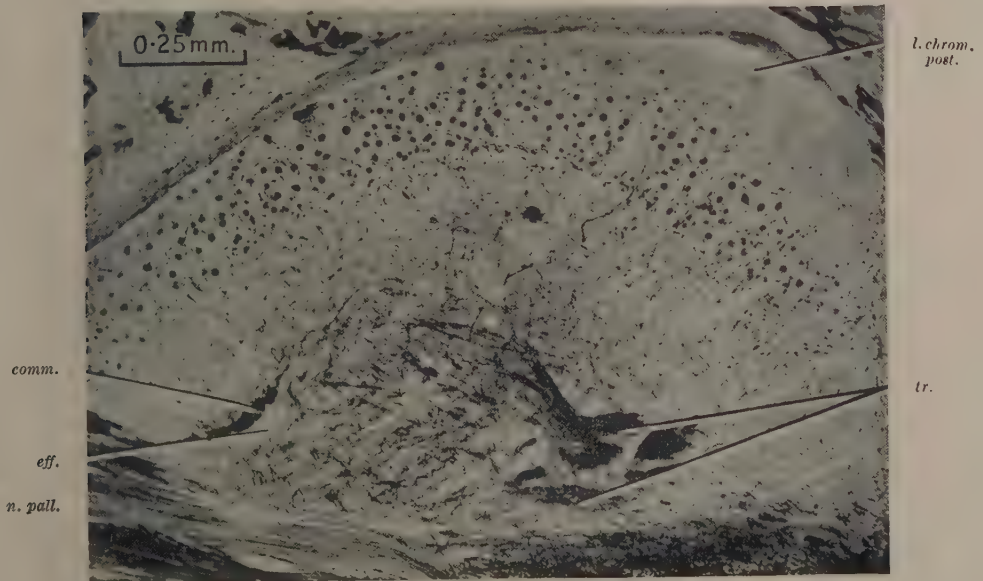
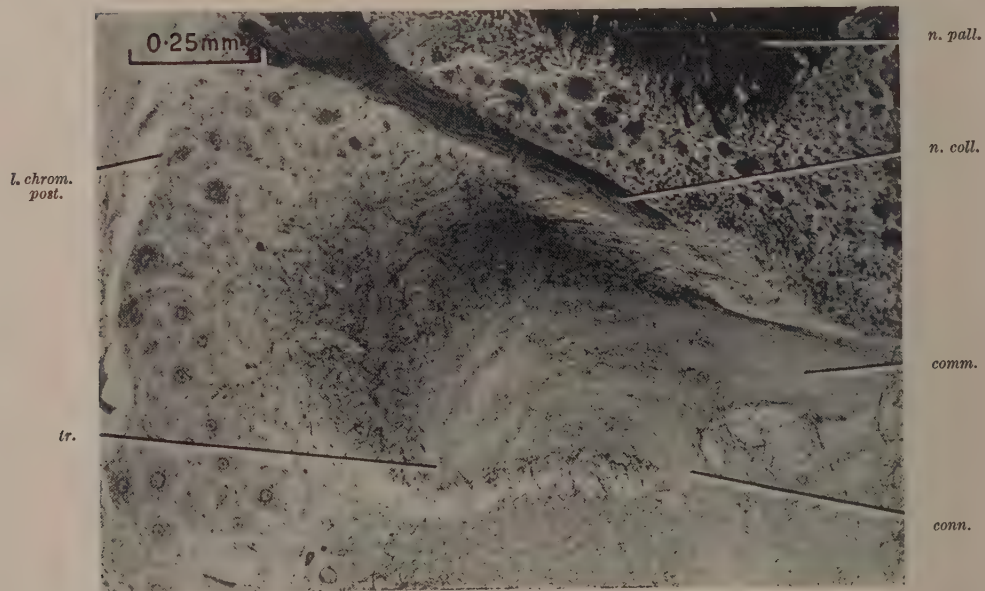


FIG. 1.—*Octopus vulgaris*.
FIG. 2.—*Sepia officinalis*.

FIG. 3.—*Argonauta argo*.FIG. 4.—*Loligo pealii*.

relationships of the afferent and efferent fibres. I have spoken superficially of both *Loligo* and *Argonauta*, saying only that their neuropil appears as a tangled mass and not saying what the fibres do. I have not done this willingly, but there are, as yet, no answers to these and other criticisms. I thought, however, that it was worth while to report briefly the point which these researches have reached. And to lay before you, a suggestion which I hope may be profitable, even if it is not very original.

C. DISCUSSION AND CONCLUSIONS.

Comparing as we have just done the neuropil of the posterior chromatophore lobe of *Octopus*, *Sepia*, *Loligo* and *Argonauta*, it is clear that the neuropils are more regularly organized in *Octopus* and *Sepia* than in *Loligo* and *Argonauta*, i.e. have a more obvious arrangement. I have already pointed out that the chromatophore system of *Octopus* and *Sepia* is organized in such a way as to produce a wide variety of complicated colour patterns, while that of *Loligo* and *Argonauta* can produce only limited and simple changes in the chromatophores. It is therefore a reasonable hypothesis that the regularity of arrangement of the neuropil of the posterior chromatophore lobes of *Sepia* and *Octopus* is to be related to the complexity of chromatophore behaviour; and the lack of regularity in *Loligo* and *Argonauta* to the simplicity of chromatophore behaviour.

In making these comparisons I am aware that I have added to my sins of histological omission by basing comparisons on such crude assessments as 'complex' and 'simple', 'regular' and 'irregular'. I doubt if anyone who has seen them would deny that the colour patterns of *Loligo* and *Argonauta* are less complex than those of *Sepia* and *Octopus*. But it is certainly dangerous to base too much on a lack of conspicuous regularity in neuropils. There must be some degree of regularity even in the most apparently unorganized of neuropils, otherwise there could presumably be no organized behaviour. I said earlier that the problem of relating different neural arrangements to differences of behaviour and of comparing different neural arrangements, was made difficult because we cannot describe the neuropils precisely. I suggest that, given a series of patterns of behaviour, such as we have been discussing, and a rough and ready assessment of the complexity of the neuropils, we can at least begin to look systematically for the quantities we need to measure to establish these relationships.

The areas innervated by the chromatophore lobes can be clearly defined. The number and types of chromatophores could be estimated. A more precise statement of the variety of patterns could be obtained. Against these data we could begin to plot a provisional assessment of the degree of regularity of the neuropil. It should not be too difficult to find measurements to qualify and perhaps disprove my present hypothesis. We might find, for example, that in *Sepia* and *Octopus* each afferent bundle of fibres came in contact with more bundles of efferent fibres than in *Loligo* and *Argonauta*; and that each efferent bundle in *Octopus* and *Sepia* was subjected to the influence of more afferent fibres than in *Loligo* and *Argonauta*. I cannot honestly say that, at the moment, these comparisons suggest very precisely the measurements that might be made. Nor do I think that, given such data as might be selected, interpretation would be easy. However, such an approach would lead to the systematic collection of data. I submit to discussion that by taking a group of animals which show a series of variations in an effector (or sensory) system and comparing these with the accompanying variations in central nervous organization, we might begin to find what further measurements are needed to make precise statements relevant to the behaviour of these and less limited systems. If such data were obtained, it is conceivable that the elucidation

and comparison of neuropils of systems more difficult to examine, such as the cerebral cortex of vertebrates and the verticalis system of cephalopods, could be more readily undertaken.

I should like to thank Professor J. Z. Young and Professor P. B. Medawar for their valuable criticisms; also the technicians of the Anatomy Department who, in their various capacities, have contributed to this paper.

REFERENCES.

- BOYCOTT, B. B. & YOUNG, J. Z. 1950. The comparative study of learning. *Symposia of the Society for Experimental Biology*, No. IV, 432-453.
 PARKER, G. H. 1948. *Animal colour changes and their neurohumours*. Cambridge: University Press.
 SANDERS, F. K. & YOUNG, J. Z. 1940. Learning and other functions of the higher nervous centres of Sepia. *J. Neurophysiol.*, **3**, 501-526.
 SERENI, E. 1930. The chromatophores of the cephalopods. *Biol. Bull., Wood's Hole*, **59**, 247-268.
 SERENI, E. & YOUNG, J. Z. 1932. Nervous degeneration and regeneration in cephalopods. *Pubbl. Staz. zool. Napoli*, **12**, 173-208.
 STEVENSON, J. A. 1934. On the behaviour of the long-finned squid, *Loligo pealii*. *Canad. Field Nat.*, **48**, 4-7.
 YOUNG, J. Z. 1951. Growth and plasticity in the nervous system. *Proc. Roy. Soc. B.*, **139**, 18-37.

EXPLANATION OF THE PLATES.

PLATE 1.

- FIG. 1.—Sagittal section of a posterior chromatophore lobe of *Octopus vulgaris* (l. chrom. post.); tr., tract from the ipsilateral lateral basal lobe joining the interchromatophore connective (conn.); comm., commissure of the posterior chromatophore lobes, this commissure has not yet been shown to contain fibres of the lateral basal lobe tract; p., pocket of darkly staining fibres protruding from the neuropil into the cell wall.
 FIG. 2.—Horizontal section of a posterior chromatophore lobe of *Sepia officinalis* (l. chrom. post.); tr., tract from the ipsilateral lateral basal lobe running across the efferent fibres, just visible as pale streaks passing diagonally from right to left. The interchromatophore connective is not visible in this section, it enters the chromatophore lobe independently of the lateral basal lobe tract; eff., efferent fibres joining the pallial nerve (n. pall.); comm., commissure of the posterior chromatophore lobes, which contains ipsilateral and contralateral lateral basal lobe fibres and fibres running between the two posterior chromatophore lobes.

PLATE 2.

- FIG. 3.—Sagittal section of a posterior chromatophore lobe of *Argonauta argo* (l. chrom. post.); tr., tract from the ipsilateral lateral basal lobe; comm., commissure between the posterior chromatophore lobes. The details of these and the interchromatophore connective are not yet known.
 FIG. 4.—Horizontal section of the posterior chromatophore lobe of *Loligo pealii* (l. chrom. post.); tr., tract from the ipsilateral basal lobe showing faintly through the darker-staining neuropil; comm., commissure between the two posterior chromatophore lobes, its constitution is not yet known; conn., interchromatophore connective entering separately from the lateral basal lobe tract; n. pall., pallial nerve; n. coll., collar nerve, which interrupts the posterior chromatophore lobe wall, but has no fibre connections with this lobe.

THE FUNCTIONS OF THE GASTROPOD STOMACH

By J. E. MORTON, M.Sc., Ph.D. Department of Zoology, Birkbeck College, and Department of Zoology, Queen Mary College, University of London.

(With 3 text-figures.)

The earliest molluscs were probably microherbivores, and as regards gut characters, the most primitive living forms are today found among the Archaeogastropoda. The stomach here is by no means simple, yet it is

reducible to a structural plan common to that of most gastropods and of other molluscan classes. In looking back to the first members of the phylum, it is probably not far wrong to imagine the stomach of the 'archae-mollusc' as being like that of a modern fissurellid, such as *Diadora* or *Scutus*. The animal must have been a creeping bottom-dweller, with a strong broad radula, raking up detritus, or perhaps cropping living algae. Mucus and cilia played the most important role in the gut, and fine particles of food passed backwards in an essentially continuous mucous string. The stomach was the most specialized part of the gut, and had three regions—a ciliary sorting area, with folds and narrow grooves, converging on the intestinal groove; an area of cuticle, raised into a stout gastric shield, serving to prevent abrasion by sharper particles; and—adjacent to the intestinal groove and freely opening to it—a style sac, lined with strong cilia beating transversely, and rotating the mucous string spirally forward from the stomach through the intestine.

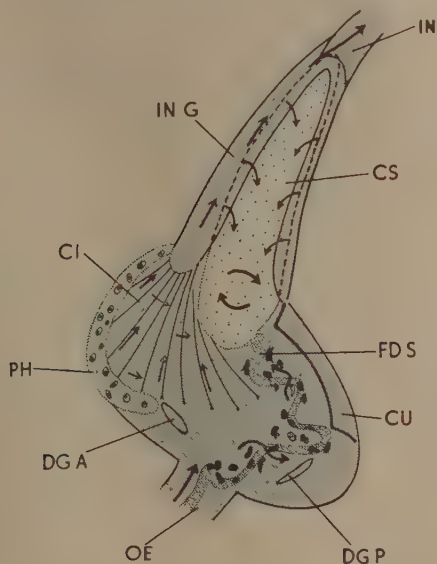


FIG. 1.

The portion of the food string within the style sac early became compacted into a 'protostyle', a rod of stiff viscid mucus, studded with faeces derived both from waste material of the digestive gland, and from larger indigestible particles rejected by the stomach. Distally, this rod became continuous with the faecal string in the intestine; and where its head projected from the style sac into the stomach, it remained attached to the food string issuing from the oesophagus. Within the stomach the food string became wound into a close-coiled spiral, and the rotating protostyle served as a capstan with three chief functions—to draw the food string into the stomach from the oesophagus by the gradual coiling and shortening of its length; to slow down the passage of light particles within the stomach to a gradual progress within the mucous string; and to sweep the loose particles in the stomach repeatedly across the surface of the ciliary sorting area. Mechanical sorting was thus probably one of the earliest functions of the molluscan stomach; and Yonge

has demonstrated (1935) that in this part of the gut, the pH is lowered to bring the mucus near its iso-electric point, rendering it less viscid, and bringing about a shedding of the load of food particles from the string, so that they become loose within the stomach and available for sorting.

Coarse material passes directly to the intestinal groove by way of the sorting area; finer particles are kept in suspension in the stomach and are destined to the paired digestive diverticula. Primitively, digestion must have been in part extracellular; oesophageal glands and pouches are present in Polyplacophora (Fretter, 1937) as well as in archaegastropods, and seem to be a truly primitive part of the molluscan foregut. After preliminary digestion, finely divided material would be received into the digestive diverticula for absorption and completion of digestion intracellularly.

From this earliest plan of the stomach with its mucous string, evolution has proceeded forward in several directions; and the evolution of function in the gastropod stomach is in large part a story of the changing nature and role of the mucous rod that is rotated in the style sac. We have elsewhere (Morton, 1951) spoken of the acquisition of the crystalline style through the loss of the faecal character of the protostyle; and the development of an enzyme store in the crystalline style is a good instance of parallel evolution in microphagous mesogastropods and lamellibranchs, both groups derived from more primitive molluscs possessing protostyles. In the style-bearing prosobranchs, the crystalline style sac remains for the most part shorter and less specialized than in the lamellibranchs. In some few forms (*Pterocera*, Yonge, 1932; *Xenophora*, Morton, 1949) it may become a 'caecum' by its complete separation from the intestine; in most cases, however, it remains open to the intestine by a narrow slit, and there are few morphological changes from the protostyle sac of more primitive forms. For while the style enzyme has been acquired independently in the two classes, the morphological features of the style sac are a common heritage from the earliest of molluscs. In gastropods with a crystalline style, ciliary currents on the typhlosole bounding the style sac are now directed downwards into the stomach, thrusting the head of the style against the gastric shield; the style is usually clear and hyaline, no longer faecal, but it retains always its connection with the oesophageal food string, which is wound into the stomach by its rotation. The role of the amylolytic enzymes of the style has been fully dealt with by Yonge (1923, 1926); in addition, from recent work (Newell, 1952) a cellulase has been reported in the styles of the oyster and the mussel, and may be more widely distributed than has been hitherto recognized. This enzyme perhaps has a link, as already suggested (Morton, 1951) with the spirochaete population of the style of many lamellibranchs, and of the protostyle of the gastropod *Murdochia* (Morton, 1952). In general, the protein matrix of the style seems to support a rich and pure flora of spirochaetes whose significance in digestion has hardly begun to be examined.

The long slit by which the style opens to the intestine is more than a survival in phylogeny; it may also play an important role in admitting to the style-sac lighter particles such as diatoms which have been too soon wafted out of the stomach before digestion is complete. These are gradually carried back to the stomach embedded in the semifluid substance of the style, which thus performs what Yonge (1926) has aptly called a 'retrieving function'.

Among many archaegastropods another type of stomach pattern is found; and though this is probably advanced upon the ideally primitive condition, it in fact occurs among the three most primitive families living today—the Trochidae, the Haliotidae, and—so far as we have adequate knowledge—in the archaic Pleurotomariidae (Woodward, 1901). Here the stomach is produced posteriorly into a long, closely coiled spiral caecum, into which the greater part of the ciliary sorting area has migrated back from the general

chamber of the stomach. The mode of action of this type of stomach is fairly easily understood by comparison with the previous description. A protostyle remains within the style sac, stiffly permeated with faeces and continuous distally with the mucous faecal string of the intestine. The connection with the food particles coming in from the oesophagus is now, however, interrupted. Food material tends to be carried straight backwards from the mouth of the oesophagus by a smooth ciliated tract along the floor of the spiral caecum as far as its tip. The roof of this caecum carries an extension of the sorting area, and particles are no longer swept across a broad sorting area by stirring within the stomach, but are brought in contact with the ciliated epithelium during their passage through the long, dorsoventrally compressed lumen of the spiral caecum. There are two outward paths from the caecum. The first—around the convex side of the caecum—carries the most finely sorted material to the single digestive diverticulum; the other—around the concave side—conveys coarser rejected material back to the general chamber of the

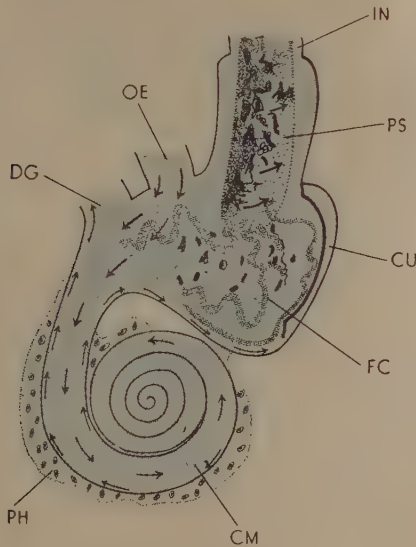


FIG. 2.

stomach, where mucous strings, one or perhaps several, become continuous with the proximal end of the protostyle. Here then the protostyle does not draw food particles into the stomach, but carries faecal threads out. In *Monodonta* Graham (1949) speaks of the sorting caecum itself as 'spinning' a long, tangled mucous string into the general chamber of the stomach.

The spiral caecum is not only a sorting area; it is also the site of a process that would appear to go hand in hand with ciliary sorting wherever it occurs in the gastropod stomach, namely the uptake of fine particles by wandering phagocytic cells which intrude into the lumen from the vascular connective tissue underlying the epithelium. Yonge (1926) has also demonstrated these cells in *Ostraea* and (1923) in the sorting area of *Mya*. They may at times, especially in the intestine, perform also a rejectory function; but within the stomach they evidently constitute an important means of non-localized intracellular digestion. Their later fate is not yet certain; they may in some cases retreat between the epithelial cells, or become cytolysed within the lumen

of the stomach and yield their partly digested contents for final absorption by the digestive gland.

One large series of prosobranchs, the higher mesogastropods and all the Stenoglossa, have become carnivorous. They are probably not wholly a monophyletic group, and we need not speak here of their stomachs in detail, since the structure becomes extremely simplified with the loss of the need to sort and mobilize a large bulk of particulate food. Such old landmarks as the style sac, typhlosoles, gastric shield and sorting area finally become entirely lost; though Graham (1949) has described well-marked relics of the earlier structure of the stomach in the carnivores *Trivia*, *Nucella* and *Nassarius*. Simplification of the stomach is accompanied by a compensating complexity of the buccal mass, introvert and secretory regions of the oesophagus.

The pulmonate and opisthobranch stomachs may also be derived from the plan of the more archaic gastropods. Both the Pulmonata and the Opisthobranchiata are very varied and specialized in their highest members. Yet they probably originated together by a single offshoot from the prosobranch stock, and in each case there is a tendency for the gut to become strongly muscular and to lose its sorting functions and its reliance on cilia and mucus. A similar transition to a muscular gut has occurred in chordates when their earliest microphagous habits were abandoned; and it is perhaps worth noting that the higher echinoderms have evolved muscular mechanisms with the loss of the particle-feeding habits that seem to have been the basal condition in this phylum also.

The stomach is a primitive maritime pulmonate such as the ellobiid *Leucophytia* may serve as typical. The greater part of the stomach here becomes a muscular-walled gizzard, which serves for triturating and churning unsorted detritus, and acts as a force pump for filling the digestive diverticulum with a semifluid suspension of food particles in mucus. The gizzard is wholly lined with cuticle. The anterior part of the stomach, connected with both oesophagus and intestine, is weakly ciliated, but the folded sorting area is entirely lost. The gizzard corresponds to the gastric shield area of the stomach, greatly enlarged. The style sac has vanished without trace in *Leucophytia*, and the beginning of the intestine is muscular and peristaltic. Yet the evolution of the pulmonate stomach has not happened suddenly or without leaving intermediate stages: in the primitive pulmonate *Otina* there are distinct traces of the sorting plicae and of a style sac with its characteristic epithelium and containing a protostyle built up of faeces from the digestive gland. In addition, the muscular gizzard is hardly yet developed (Morton, 1952 a). In most ellobiids and other pulmonates a posterior caecum is retained as a vestige, indicating that it may indeed be a fundamental feature of the earliest gastropod stock. In *Leucophytia* this caecum has become secondarily everted into the gizzard to act as a valve controlling the movements of stomach contents. In other pulmonates, such as *Lymnaea*, the caecum retains something of its sorting role, and secretes a portion of the faecal string, consolidating a cord of mucus and passing it gradually into the intestine where it becomes intertwined with the gizzard faeces and 'liver strings' (Carriker, 1946).

In the earliest opisthobranchs (tectibranchs) there is much the same functional pattern as in these pulmonates, though the morphological story is different. Here the gizzard is not only heavy-walled and muscular; its lining is equipped with strong calcareous teeth. The opisthobranch gizzard is, however, derived from the posterior part of the oesophagus and is not structurally homologous with the pulmonate stomach. It serves for comminuting detritus as in *Haminea* and *Philina*, or, to some extent—in *Scaphander*, for crushing shells of small bivalves preyed upon. In *Haminea* the stomach itself (Fretter, 1939) has sorting ridges and cuticle reminiscent of the prosobranchs; it later becomes merely a small annexe to the digestive

diverticula—usually three in number in opisthobranchs—lying behind the muscular oesophageal gizzard. In many tectibranchs such as *Aplysia* (Howells, 1942) and in a number of dorid nudibranchs (Forrest, 1951), (Millott, 1937), a posterior caecum remains. From the evidence of its histology, it evidently corresponds not to the sorting caecum but to the original style sac which has here quite lost its function of rotating a string of stomach contents, and has returned to the simple role of fashioning a faecal rod. In the fissurellid *Diadora* the style sac fashions a mass of sponge spicules in almost identical fashion with the caecum of the dorid *Jorunna*. Such a caecum is present also in the thecasomatous pteropods (Howells, 1936)—where in *Cymbulia* a tiny style is rotated within the true stomach behind the gizzard. The survival of a gizzard in these ciliary feeding opisthobranchs is a puzzling feature that one hesitates to explain on phylogenetic grounds alone; in

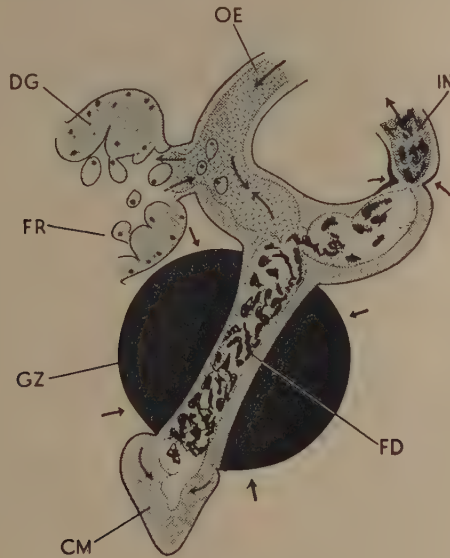


FIG. 3.

Limacina (Morton, unpublished) the toothed gizzard serves as a tiny mill for crushing the cases of diatoms and for pumping a two-way flow to and from the digestive diverticulum.

Not many opisthobranchs are rapacious carnivores; but where an economic protein diet of small bulk allows (whether plant or animal) the stomach may become reduced and greatly simplified, as in the two groups—the suctorial doridomorphs (Forrest, 1951) which are carnivorous, and in the Ascoglossa which feed by piercing algal cells. Finally, the little *Calma*, which lives on the yolk of fish eggs has reduced its gut to the extreme of simplification; there is neither gizzard nor functional stomach and the anus becomes closed, the small amounts of faecal waste accumulating in the liver cells during the whole life of the animal.

With the loss of their access through the ciliary sorting area, amoebocytes from the blood vessels have come to play little part in digestion in pulmonates and opisthobranchs. There is still, however, in the more primitive detritus

feeders such as the Ellobiidae and the tectibranchs, the problem of a large bulk of food suspended in mucus and requiring a large absorptive surface and thorough penetration by enzymes. With the loss of the wandering amoebocytes, this need is in part met by the bulging of the digestive cells into the lumen, becoming rounded and club-shaped and almost surrounded by mucus-bound food. Finally, the tips of these cells become completely constricted off into the lumen and in ellobiids and *Otina* (Morton 1952 a) as well as in nudibranchs (Millott, 1937; Forrest, 1951) a whole cell may thus round off and detach itself—nucleus included—and wander freely through the mucous contents of the stomach and diverticulum. These cells appear to function just as do the amoebocytes from the blood vessels; the writer has elsewhere suggested for them the term 'fragmentation phagocytes'.

REFERENCES.

- CARRIKER, M. R. 1946. Morphology of the Alimentary Canal of the Snail *Lymnaea stagnalis appressa* Say. *Trans. Wis. Acad. Sci. Arts. Lett.*, **38**, 1.
- FORREST, J. E. 1951. Feeding Habits of some British Dorid Nudibranchs. *Contrib'n., Section D., Brit. Ass. Adv. Sci.*, 1951.
- FRETTER, VERA. 1937. The Structure and Function of the Alimentary Canal of some species of Polyplacophora (Mollusca). *Trans. roy. Soc. Edinb.*, **59**, 119.
- . 1939. The Structure and Function of the Alimentary Canal of some Tectibranch Molluscs with a Note on Excretion. *Trans. roy. Soc. Edinb.*, **59**, 599.
- GRAHAM, A. 1949. The Molluscan Stomach. *Trans. roy. Soc. Edinb.*, **61**, 737.
- HOWELLS, H. H. 1936. Anatomy and Histology of the Gut of *Cymbulia peronii* (Blainville). *Proc. malac. Soc. Lond.*, **22**, 62.
- . 1942. The Structure and Function of the Alimentary Canal of *Aplysia punctata*. *Quart. J. micr. Sci.*, **83**, 357.
- MILLOTT, N. 1937. On the Morphology of the Alimentary Canal, Process of Feeding and Physiology of Digestion of the Nudibranchiate Mollusc, *Jorunna tomentosa* (Cuvier). *Phil. Trans. (B)*, **228**, 173.
- MORTON, J. E. 1949. The Adaptations of *Xenophora*, the Carrier Shell. *N.Z. Sci. Rev.*, **7**, (10), 188.
- . 1951. The Role of the Crystalline Style. *Proc. malac. Soc. Lond.*
- . 1952. A Preliminary Study of the Land Operculate *Murdochia pallidum* (Cyclophoridae: Mesogastropoda). *Proc. roy. Soc. N.Z.*, 80.
- . 1952 a. The Functional Morphology of *Otina otis* Turton, a primitive Marine Pulmonate. In the Press.
- NEWELL, B. S. 1952. A cellulolytic enzyme in *Ostraea edulis*. *J. Mar. biol. Ass. U.K.*, **32**, i.
- WOODWARD, M. F. 1901. The Anatomy of *Pleurotomaria beyrichii* Hilg. *Quart. J. micr. Sci.*, **44**, 215.
- YONGE, C. M. 1923. The Mechanism of Feeding, Digestion and Assimilation in the Lamellibranch *Mya*. *J. exp. Biol.*, **1**, 15.
- . 1926. The Structure and Physiology of the Organs of Feeding and Digestion in *Ostraea edulis*. *J. Mar. Biol. Ass. U.K.*, **14**, 295.
- . 1932. Notes on Feeding and Digestion in *Pterocera* and *Vermetus* with a discussion on the occurrence of the crystalline style in Gastropoda. *Sci. Rep. G. Barrier Reef Exp. Brit. Mus. (Nat. Hist.)*, **1**, 259.
- . 1935. On some aspects of digestion in ciliary feeding animals. *J. Mar. biol. Ass. U.K.*, **20**, 341.

**PROCEEDINGS OF THE GENERAL MEETING HELD
8 May 1952**

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 24 April 1952, having been circulated, were taken as read, and confirmed.

The PRESIDENT welcomed the presence at the Meeting of His Excellency the Colombian Ambassador.

The following were thanked for gifts made to the Library since the last Meeting :—The Directors of the Holland Society of Sciences.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Professor Charles Geddes Coull Chesters, M.Sc., Ph.D., Dr. Aleksandrs Melderis, Dr. Mahmoud Ahmed Melouk and Mr. Derek Oliver Weitzel, B.Sc.

Certificates of recommendation for election of Associates *honoris causa* and an Ordinary Associate were read for the first time in favour of the following : Associates *honoris causa* :—The Rev. Dr. Stanley Graham Brade-Birks, Humphrey Gilbert-Carter and George W. Robinson. Ordinary Associate :—Miss Margaret Wickson.

Certificates of recommendation for election of Fellows and Foreign Members were read for the second time in favour of the following : Fellows :—Mrs. Antoinette Nellie Gibby, B.Sc., H. E. Goto and Thomas James Walsh, Ph.D. Foreign Members :—Prof. Dr. Lothar Geitler and Dr. Ernst Mayr.

Colour films of Mexico and South America taken during 1939 and 1948–51 whilst on Potato research and collecting expeditions were shown by Dr. J. G. Hawkes, who also gave a commentary on the films.

Abstract,—

SOUTH AMERICA. This film, taken in 1939 during the Commonwealth Agricultural Bureaux Potato Collecting Expedition to the Andes of South America, shows views taken in Argentine, Bolivia, Peru and Ecuador, not only of the scenery and natural vegetation of these lands but of the Indians and their primitive agricultural methods. The expedition collected samples of wild and cultivated potatoes for breeders in Great Britain and the Commonwealth, besides dried plant material for Kew and other herbaria.

COLOMBIA: Filmed in 1948 to 1951 during development of a potato research programme for the Government of Colombia. Shots of the high Andean vegetation zones, potato cultivation and other typical features of Colombia are included.

A short visit was also made to the neighbouring republic of Venezuela.

MEXICO. Taken in 1949 when the speaker made a four-month potato collecting expedition to Mexico for the Commonwealth Agricultural Bureaux. The contrasts between Mexico and South America were pointed out with regard to the natural vegetation. The film also includes shots of archaeological remains and some of the more primitive Indian tribes with their typical food plants.

**PROCEEDINGS OF THE ANNIVERSARY MEETING HELD
24 May 1952**

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 8 May 1952, having been circulated, were taken as read, and confirmed.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Mrs. Elsie H. Purnell, M.A., Douglas Graham Cowden, B.Sc., Hubert Frederick Dovaston, Prafulla Chandra Sharma, M.Sc., and Miss Frances Pitt.

Candidates for membership were balloted for and elected :—

Fellowship.—Mrs. Antoinette Nellie Gibby, B.Sc., H. E. Goto, B.Sc., and Thomas James Walsh, Ph.D.

Foreign Members.—Professor Dr. Lothar Geitler and Dr. Ernst Mayr.

Associates honoris causa.—The Rev. Dr. Stanley Graham Brade-Birks, Humphrey Gilbert-Carter, M.A., M.B., Ch.B., and George W. Robinson.

Ordinary Associates.—Miss Olga Holbek and Miss Margaret Wickson.

The Bye-Laws regulating the Election of Council and Officers having been read by the General Secretary, the President declared the Ballot for new Members of Council to be open, and voting began. The President thereafter appointed Mr. A. L. Goodday, Mrs. Vera Higgins and Mr. R. H. Jeffers as Scrutineers of the Ballot.

The Ballot was closed at the due time, and the result declared to the Meeting.—NEW MEMBERS OF COUNCIL :—Mr. J. E. Dandy, Dr. S. M. Manton, F.R.S., Professor P. B. Medawar, F.R.S., Mr. E. Milne-Redhead and Dr. W. E. Swinton.

(The retiring Councillors were Dr. B. Barnes, Mr. Gerald A. Best, Sir Norman B. Kinnear, C.B., Dr. C. F. A. Pantin, F.R.S., and Mr. N. Y. Sandwith.)

The PRESIDENT declared the Ballot of Officers to be open and voting began. The Ballot was closed at the due time, and the result declared to the Meeting.—OFFICERS.—*President* : Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S. ; *Treasurer* : Colonel F. C. Stern, O.B.E., M.C. ; *Zoological Secretary* : Dr. A. Tindell Hopwood ; *Botanical Secretary* : Dr. George Taylor.

In handing the Linnean Gold Medal to Mr. I. Henry Burkill, F.L.S., the PRESIDENT spoke as follows :—

Mr. Burkill : In awarding to you the Linnean Gold Medal, the Society honours a Fellow conspicuous in research, and one who has always had its interests keenly at heart. Joining the Society as far back as 1894, you have twice served on its Council, have on two separate occasions been a vice-President, and acted as Botanical Secretary from 1937 to 1944, helping to guide the affairs of the Society during one of the most critical periods of its existence. Already when a student at Caius College, Cambridge, you commenced, with J. C. Willis, those studies on geographical distribution and dispersal of plants which were to be so full of valuable results to science. This early work entailed climbing several thousand of the pollard willows on the banks of the Cam and Ouse in order to compare their epiphytic flora with that of the surrounding district. The results, published in the *Proceedings of the Cambridge Philosophical Society* in 1895, also included an account by you of plant-dispersal through the agency of the Cambridge dust-carts which displayed the rôle of man in distributing seeds within an urban environment.

After graduating in 1891 you were appointed Assistant Curator of the University Herbarium at Cambridge, a post which you held until you joined the Kew staff in 1897, becoming Principal Assistant in 1899. In 1907 you became a member of the Economic Survey of India at Calcutta, where as Assistant Reporter you collaborated with Sir George Watt. From 1912 to

1925 you were Director of the Botanic Garden at Singapore, during which your many-sided interests in tropical plants matured. A product of this period is the widely used *Dictionary of the Economic Plants of the Malay Peninsula*, published in 1935.

Since your release from administrative duties in 1925, you have been able to devote your life to most fruitful research. Among the many important contributions, which you have made to botanical science, are the studies on the taxonomy, morphology, and distribution of the Old World species of *Dioscorea*. This many-sided and scholarly work displays the enthusiasm and tenacity with which you have followed up the wider implications of your researches. They have led you to study the vernacular names in a number of languages, to consider diverse cultural contacts, and to examine various aspects of the origins of cultivated plants, as well as to undertake the detailed investigation of the life-history of the British *Tamus communis*. Those of us who were privileged to listen to the Hooker Lecture, which you delivered in these rooms in November last, will be able to appreciate to the full the profundity of the studies you have undertaken on the distribution of economic plants within the Tropics.

We welcome with great pleasure the inclusion of your name among the many distinguished recipients of the Linnean Medal.

In reply, Mr. Burkill expressed his profound appreciation of the honour that had been conferred upon him.

THE PRESIDENT'S REVIEW

The 164th session, which terminates to-day, has been marred by the great loss sustained by the Society through the death of its revered Patron, His Late Majesty King George VI. The Fellows met in General Meeting on 7 February of this year under the shadow of His Majesty's sudden and unexpected decease which had been announced on the previous day. After reading Addresses of Condolence with Her Majesty the Queen, Her Majesty the Queen Mother and Her Majesty Queen Mary, all present standing, the Meeting adjourned without proceeding to further business. With the rest of the nation we deeply mourn the loss of a beloved monarch who knew so well how to fulfil the arduous duties his position required of him. Her Majesty Queen Elizabeth the Second can be assured of the devotion and loyalty of the Officers and Fellows of the Linnean Society.

We also have to deplore the loss by death of four of our Foreign Members :—Johannes Gossweiler, Dr. Ole Theodor Jensen Mortensen, Prof. Emile Topsent and Dr. Thomas Wayland Vaughan. It was only last year that the Society recognized Dr. Mortensen's great services to zoological science by awarding him the Linnean Gold Medal. Twelve of our Fellows, many of them of long standing, have died during the session. Prof. F. T. Brooks, who had attained great distinction as a mycologist, served on the Council from 1941 to 1944 and was a Vice-President during the session 1933-34.

Our meetings have continued to provide much interesting matter. On 22 November Mr. Burkill delivered the Hooker Lecture on the "Origin of the Cultivated Plants of the Old World" to an audience which showed, by its size and its rapt attention, the deep interest aroused by the speaker's topic. There were two excellent symposia, one dealing with Photoperiodism, the other with Form and Function in the Mollusca, both illustrative of rapid advance in their respective branches of science and both productive of lively discussions; our thanks are due to Prof. F. G. Gregory and Prof. A. Graham, who bore the chief burden of organizing these symposia. A joint discussion with the Systematics Association again took place on 20 March. At the first meeting of the Session Mr. Kingdon-Ward gave a graphic account of his experiences

in the Lohit Valley in 1950, while on 8 May Dr. J. G. Hawkes showed a most striking series of colour films of Mexico and South America. If I add that our programme has included communications by Prof. S. Zuckermann on the Skull of Apes and by Dr. Edney on British Woodlice, I shall have given a sufficient indication of its diversity. As an outcome of Mr. Kingdon-Ward's paper the Council decided to draw the attention of the Botanical Survey of India to the great importance they attached to a continued exploration of the Lohit Valley. We have since been informed that the Survey is taking steps to encourage such exploration.

The reception on 6 December was quite as successful as those of preceding years. Dr. Pantin's film "The Behaviour of a Sea Anemone" aroused great interest, and we are greatly indebted to him, in view of his many preoccupations, for having spared the time to come and show it in person. The exhibits attained the usual high standard, and it would be invidious to select any one for special mention.

We are greatly indebted to Dr. J. G. Cockburn for the permanent loan of a film-projector which proved its value at our last meeting. One of our deceased Fellows, Mr. James Inch, has bequeathed to the Society a valuable library, comprising upwards of 250 volumes, of works on tea, while Mr. J. H. Robin has given to us the collected correspondence of Dr. Richard Pulteney, F.R.S., F.L.S. Among the many notable accessions to the library, I may specially mention the English Translation of Knut Hagberg's book on Linnaeus. This will be of great interest to our Fellows, and it is gratifying to the Society to read the appreciative words in the Epilogue as to the care with which they have preserved the Linnean Collections for more than a hundred years. It is appropriate to mention at this point that early in the session the Council appointed a Committee to make recommendations for the care and readier utilization of the Society's collections. After two meetings the Committee presented a report to the Council in which a number of proposals were made, some of which are still under discussion. The Council, however, decided that, in addition to the two Secretaries, there should be two Honorary Curators of the Collections and have appointed Mr. N. Y. Sandwith and Mr. W. H. T. Tams as the first Honorary Curators.

His Majesty King Gustav VI Adolf of Sweden has signed the illuminated vellum sheet which has been inserted in the Roll and Charter Book of the Society. It is a pleasure to note that for the first time the number of Fellows is well above the 800 level. In conjunction with the Royal Society, the Royal Geographical Society, and the Zoological Society, steps are being taken to have a memorial plaque affixed to the house in Broadstone, Dorset, in which Alfred Russell Wallace, O.M., F.R.S., died.

At the Annual Dinner of the South London Entomological and Natural History Society on 26 October the Linnean Society was the Guest-Society and was represented by the President and the Honorary Secretaries. Dr. Pantin has been nominated as the Society's representative to serve on the British National Committee for Biology from 1 January, 1952, for six years. The Clerk, Miss Holberton, resigned at the end of last year and Mrs. Edith Ziegler has been appointed in her place.

During this session the Council has departed from the practice followed for some years of having only a single ballot for the Election of new Fellows and balloting has taken place in November and April.

There has been delay in the issue of publications, and only one number of the *Proceedings* and none of either *Journal* has appeared during the session, although parts of all three are in an advanced stage and will be published very shortly. It has been decided to issue Dr. Hugh Scott's paper on "The Gughé Highlands of Ethiopia" as Part 3 of Vol. 163 of the *Proceedings*, Dr. Scott having generously agreed to bear a major part of the costs involved.

A further part of the *Transactions* containing reports of the Percy Sladen Memorial Expedition to Lake Titicaca in 1937 is in preparation, as well as a number dealing with woodlice in the series of Synopses of the British Fauna.

Once again our rooms have been used by many kindred Societies. Some of our premises, including the Old Council Room and the Meeting Room are to be redecorated during the coming summer.

There is nothing new to report respecting the proposals for rehousing the Scientific Societies and, under existing circumstances, progress must be slow.

With the conclusion of this meeting I shall terminate my three years of office as your President, and I would like to take this opportunity of expressing to my Fellow-Officers, past and present, to the Members of Council who have served under me, and to the Fellows as a whole my deep gratitude for the invariable courtesy with which they have treated me.

TREASURER'S REPORT

Printed copies of the Accounts for the financial year which ended on 30 April 1952 are before you. For comparison, the figures for last year are printed in italics on the left-hand side. A statement has been prepared by the Auditors who certify as to details; the Audit-Committee has inspected the books, verified the investments and bank balances and passed the accounts; the action of the Committee has been confirmed by the Council.

I will briefly go through the accounts and deal with the main items:—

On the Income Side.

The Annual Contributions are higher than last year owing to an increased number of Fellows and from the receipt of arrears of contributions from Fellows abroad.

The Sales of Publications are considerably down on last year, but the reason for this is that our publications are late in being issued this year, owing to printing difficulties and also to the fact that some of the authors of the papers were abroad and the proofs took a long time to return. But we have definite orders for some £250 worth of Publications as soon as they are published, which we hope will be shortly.

The Society again received from the Royal Society the sum of £750 from the *Parliamentary-grant-in-aid for Publications*. We are deeply grateful for this help to our funds for expenditure on Publications.

You will see that we have not been able to make any Reserve this year from our surplus-income for Publications as we usually do mainly because many of our expenses are higher and also—as I have said previously—the income from the sale of Publications has not yet come in. There is—as you know—a *Reserve for Publications* which stood at £2,616. The Society has paid the whole of the costs of Publications up to date, which includes all those Publications which should have been issued this year and will be issued in the near future; it has, therefore, been necessary to draw £372 from the Publication Reserve Fund, which leaves the Reserve-Fund at £2,243.

On the Payment Side.

Coal and Electric Current, and Gas has cost more.

Repairs are again high owing to the final instalment of the Central Heating having been paid in this year.

Miscellaneous Printing and Stationery is very much higher, but again that is because it contains the Printing for one-and-a-half and not for one year, owing to the accounts for the half year ending May 1951 not coming in. This should be considerably lower next year.

Petty Expenses and Postages.

The figure is higher owing to higher postage-cost, etc., and increased fee to our Auditor.

The Cost of Publications is about the same as last year.

With regard to *Salaries and Wages*, this now includes the pension paid by the Society to Mr. Savage. The cost of *Staff Annuities* is considerably higher. Staff Annuities were taken out for two additional Members of the Staff, one of whom has since left the service of the Society; next year this item will be £108.

Library Account.

The Account has a balance of £208 after paying the usual items.

Library Restoration Fund.

This Fund now has a Balance of £1,036 out of £3,380 which has been subscribed. The Binding and Repairs to books since first it was formed, amount to about £1,367, the purchase of foreign works that were missing in our sets, £374, and extra shelving has cost £610.

The Society has received only £30 towards this fund this year, and I should like again to appeal to all friends of the Linnean Library to help this Fund in any way they can by donations or by legacies, in order that this historic and valuable Library can be maintained and conserved, as it should be.

Trust and Reserve Funds.

I have already mentioned the Publication Reserve, and there is no more to report on the Trust and Reserve Funds.

Investments.

The only change in the Investments is the addition of a nominal investment of £109 8s. 7d. 3½% War-loan, which is the Investment of the Composition Fees.

Annual Contribution under Covenant.

At our last Anniversary Meeting I mentioned that the Income Tax Authorities had informed us that by virtue of its status the Society is able to reclaim the Tax paid by a Fellow on the amount of his or her Annual Contribution paid under Covenant. 93 Fellows have made 7 years' Covenants which will bring an increase of some £300 in the next financial year. It is very much to be hoped that as many Fellows as possible will sign this Covenant which will make no difference to their income but will make a great difference to the income of the Society. Deeds of Covenant can be obtained from the General Secretary.

I should like to thank our General Secretary, Mr. O'Grady and our Clerk, Mrs. Ziegler, for the excellent manner in which the accounts have been kept, and for the conscientious way in which the work has been done.

If any Fellow wishes to ask any questions on these accounts, I will do my best to answer them.

On a motion by Dr. B. BARNES, seconded by Mr. C. E. HUBBARD, the Report and Statements of Accounts were adopted.

**Special Accounts
(Trust and Reserve Funds)**

[illegible]

* Including £2955 15s. 4d. in Post Office Savings Bank.

TREASURER'S ACCOUNTS FOR THE
(Presented at the Anniversary
Receipts and Payments of the Linnean Society

		General	
1950-51		1951-52	
£	RECEIPTS	£ s. d.	£ s. d.
	To Balance at 1 May 1951 :—		
	Current Account at Bank	173 4 6	
	Deposit Account Post Office Savings Bank ..	481 6 9	
	Cash in hand	12 9 10	
	Awaiting Investment	23 0 0	
729			690 1 1
96	„ Admission Fees		108 0 0
	„ Arrears of Annual Contributions	68 0 0	
	„ Annual Contributions for year	2706 12 0	
	in advance	62 3 3	
2740			2836 15 3
20	of Associates		21 19 0
164	„ Composition Fees	76 0 0	
342	„ Interest on Investments (including Income Tax recovered) ...	341 14 0	
120	Post Office Savings Bank Account	122 14 6	
	„ Sales of Publications :—		
	Transactions	57 8 1	
	Journals	169 1 6	
	Proceedings &c.	140 14 6	
603			367 4 1
750	„ Grants in aid of Publications : Royal Society ...	750 0 0	
50	<i>Mrs. E. W. Sexton</i>		
	<i>Dr. S. M. Manton</i>	5 0 0	
			755 0 0
33	„ Miscellaneous Receipts	31 3 7	
431	„ Transfer from Reserve for Publications Fund	372 11 5	
100	„ Bequest.— <i>Miss E. F. Noel</i>		
1	„ <i>War Damage Account</i>		
431	„ <i>Transfer from Reserve Fund</i>		
£6611			£5723 2 11

		Library	
£		£ s. d.	
132	To Balance at 1 May 1951	148 6 4	
85	„ Interest on Investments (including Income Tax recovered) ...	78 11 10	
11	„ Donation : <i>Imperial Chemical Industries</i>		
10	<i>John Innes Horticultural Institution</i>	10 0 0	
300	„ Transfer from General Account	300 0 0	
1	„ <i>Miscellaneous Receipts</i>		
£539			£536 18 2

		Library	
£		£ s. d.	
1713	To Balance at 1 May 1951 :—	1195 14 1	
24	„ Donations : Fellows and Friends	30 4 0	
£1737			£1225 18 1

		Fellows' Postal	
£		£ s. d.	
50	To Balance at 1 May 1951	50 6 5	

YEAR ENDED 30 APRIL 1952

Meeting, 24 May 1952)

from 1 May 1951 to 30 April 1952

Account

1950-51			1951-52
£	PAYMENTS	£ s. d.	£ s. d.
176	By Coal, Electric Current, and Gas		196 6 10
751	„ Repairs : Sundry		280 10 8
90	„ Taxes and Insurance		89 10 3
277	„ Miscellaneous Printing and Stationery		459 10 0
281	„ Petty Expenses and Postages		359 7 4
	„ Publications :—		
	Printing	1315 9 0	
	Distribution	85 14 11	
	Illustrations	176 7 6	
1671			1577 11 5
500	„ <i>Transfer to Reserve for Publications Fund</i>		
1580	Salaries, Wages and Pension		1594 19 9
15	„ 'Zoological Record' (Vol. 87) Donation		15 0 0
1	„ <i>Richard Spruce Plaque—Donation</i>		
2	„ International Union for Nature Protection—Donation		2 2 0
62	„ Staff Annuities (Annual Premiums)		203 14 5
181	„ <i>Investment of Compounders' Fees</i>		
	„ Do. Purchase of £109 8s. 7d. 3½ per cent War Loan		95 0 0
34	„ Linnean Medal		34 11 8
300	„ Transfer to Library Account		300 0 0
	„ Balance at 30 April 1952 :—		
	Current Account at Bank	8 8 11	
	Deposit Account Post Office Savings Bank ..	476 12 8	
	Cash in hand	5 17 0	
	Amount awaiting Investment	24 0 0	
690			514 18 7

£6611

£5723 2 11

Account

£		£ s. d.	£ s. d.
158	By Periodicals		198 13 4
152	„ Binding		35 10 6
75	„ Books		93 16 9
6	„ <i>Miscellaneous</i>		
	„ Balance at 30 April 1952 :—		
	Current Account	108 17 7	
	Deposit Account Post Office Savings Bank ..	100 0 0	
148			208 17 7
<u>£539</u>			<u>£536 18 2</u>

Restoration Fund

£		£ s. d.	£ s. d.
344	By Purchase of Foreign Works		
196	„ Binding and Repairs to Books		189 10 2
1	„ <i>Miscellaneous</i>		
	„ Balance at 30 April 1952 :—		
	Current Account at Bank	5 17 5	
	Deposit Account at Bank	30 10 6	
	Deposit Account Post Office Savings Bank ..	1000 0 0	
1196			1036 7 11
<u>£1737</u>			<u>£1225 18 1</u>

Account

£		£ s. d.
<u>50</u>	By Balance at 30 April 1952	<u>50 6 5</u>

Investments on 30 April 1952

General Account

£	s.	d.		Market Value 30 April 1952. £	s.	d.
1000	0	0	3½ per cent. London County Consolidated Stock 1958-68	@ 91½	915	0 0
1548	8	9	British Transport 3 per cent. Guaranteed Stock 1978-88	@ 77½	1200	0 9
109	8	7	3½ per cent. War Loan, 1952 or after	@ 77½	84	16 2
434	8	7	3½ per cent. War Loan, 1952 or after	@ 77½	336	13 8
1000	0	0	2½ per cent. Defence Bonds	@ 100	1000	0 0
2199	18	6	4 per cent. Australian Stock 1961-64	@ 99½	2183	8 6
200	0	0	3 per cent. War Stock 1955-59	@ 98½	197	0 0
1139	13	0	3 per cent. Savings Bonds 1955-65	@ 91½	1042	15 7
3260	1	3	2½ per cent. Consolidated Stock	@ 60	1956	0 9
176	19	3	3 per cent. Savings Bonds 1960-70	@ 85	150	8 4
274	5	5	3 per cent. Treasury Stock	@ 68½	187	3 9
				£9253	7	6

Library Account

£	s.	d.		£	s.	d.
471	18	9	British Transport 3 per cent. Guaranteed Stock 1978/88 (Bentham Bequest)	@ 77½	365	15 0
103	12	5	Surrey County 3 per cent. Stock 1961-66 (Wakehurst Bequest)	@ 87½	90	13 4
191	12	7	4 per cent. Australian Stock 1961-64 (Walker & Morey Bequests)	@ 99½	190	3 10
107	2	1	2½ per cent. Consolidated Stock (Stabbing Bequest)	@ 60	64	5 3
530	0	0	3 per cent. Savings Bonds 1960-70 (Taggart Bequest)	@ 85	450	10 0
1414	7	11	2½ per cent. Consolidated Stock (Flintoff Bequest)	@ 60	848	12 9
				£2010	0	2

Special Accounts

£	s.	d.		£	s.	d.
£1063	10	7	Metropolitan Water Board 3 per cent. "B" Stock (Westwood Bequest)	@ 73	169	10 8
			" " " (Hooker Lecture Fund)	@ 73	487	8 6
			" " " (Goodenough Fund)	@ 73	119	8 1
			2½ per cent. Consolidated Stock (Crisp Award Fund)	@ 60	334	1½ 3
			" " " (Westwood Fund)	@ 60	93	16 8
			" " " (Hooker Lecture Fund)	@ 60	44	16 8
£380	10	6	" " " (Goodenough Fund)	@ 60	89	13 3
			3 per cent. Savings Bonds 1955-65 (Staff Pension Fund)	@ 91½	269	11 2
			" " " 1955-65 (Staff Pension Fund)	@ 91½	8	11 8
			" " " 1960-70 (Minchin Fund)	@ 85	85	0 0
			" " " 1952 or after (Trail Award Fund)	@ 77½	79	4 0
				£1781	11	6

F. C. STERN, *Treasurer*.

We have (in conjunction with the Professional Auditors, who certify as to all details) audited the Accounts of the Society for the year ended 30 April 1952 and found them correct. We have verified the Investments and Bank Balances.

13th May 1952.
W. B. KEEN & Co., *Chartered Accountants*,
Finsbury Circus House,
Blomfield Street, London, E.C.2.

H. R. HEWER,
GEORGE TAYLOR,
A. TINDELL HOFWOOD,
W. E. SWINTON,
FRANK W. JANE,
VERA HIGGINS, } *Audit Committee*.

GENERAL SECRETARY'S REPORT

List of the Society.

Since the last Anniversary Meeting the Society has lost 29 members. The detailed statement is as follows :—

12 Fellows by death :

Wilfred Eade AGAR.	Thomas Bainbrigge FLETCHER.
Austin Edward ARMITAGE.	James INSCH.
Wilfred Ernest Watson BAKER.	Walter Samuel MILLARD.
Anthony BELT.	Stephen King MONTGOMERY.
Frederick Tom BROOKS.	Wilfred Mark WEBB.
Walter Robert Ivimey COOK.	Maud WILLIAMS.

4 Foreign Members by death :

Johannes GOSSWEILER.	Emile TOPSENT.
Ole Theodor Jensen MORTENSEN.	Thomas Wayland VAUGHAN.

2 Associates honoris causa by death :

John McConnell BLACK.	Frederick James PITTOCK.
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5 Fellows by Withdrawal :

Winifred Elsie BRENCHLEY.	Elisabeth Anna ULLMANN.
Edgar PICKARD.	Vero C. WYNNE-EDWARDS.
Edward Kemp TOOGOOD.	

6 Fellows Removed for non-payment of Annual Contributions :

David Darius HAYNES.	Quadir Hosain QURESHI.
Balai Chand KUNDU.	John Edquard SENARATNA.
Hirendra Kumar NANDI.	Geoffrey TANDY.

During the Session, 38 Fellows, 2 Foreign Members, 3 Associates *honoris causa* and 12 Ordinary Associates have been elected. The number of Fellows on the List is 800 with a further 15 Fellows elected but not yet qualified : Foreign Members 48, Associates *honoris causa* 24 and Ordinary Associates 30.

The Library.

Between 1 May 1951 and 30 April 1952, 29 books have been purchased, 22 books, 149 parts of periodical publications and 52 reprints have been presented. In addition the Society has received a library of works on Tea, comprising some 250 volumes and parts bequeathed by James Insch, F.L.S.

During the same period the number of volumes bound was 180 and 134 volumes have been repaired.

The number of volumes borrowed was 1,724—by Fellows and Associates 1,052 and 672 by the National Central Library.

706 signatures were recorded in the Library Visitors' Book.

The Linnaean and Smithian Collections.

During the past year the Collections have been consulted on more than 40 occasions. Mr. Savage is continuing with the compilation of the Catalogue of the Smithian Herbarium.

The PRESIDENT then delivered his Address on "Comparative Studies in a Polyphyletic Group : The Desmidiaceae".

On its conclusion, Dr. JOHN RAMSBOTTOM, O.B.E., moved "That the President be thanked for his excellent Address, and that he be requested to allow it to be printed and circulated amongst the Fellows". The motion was seconded by Dr. W. E. SWINTON, and being put to the meeting was carried with acclamation.

Thereafter the PRESIDENT declared the Session of 1951-52 closed.

PRESIDENTIAL ADDRESS

COMPARATIVE STUDIES IN A POLYPHYLETIC GROUP, THE DESMIDIACEAE.

(With nine groups of figures and two tables.)

In last year's address I summarized the results of a comparative study of progressive cell-differentiation among simple forms of multicellular plants. To-day I propose to deal with one of the many groups of one-celled plants, which often display an astounding range of form. Nowhere is this more striking than in the well-defined group known as the desmids. The bewildering variety of shape and often complex ornamentation of these unicellular green algae have long made them a fascinating subject of study to microscopists, who have indeed contributed much to our knowledge of these forms. Many memoirs published by this and other British Societies have dealt with the desmids of the British Isles and of other parts of the world, while foreign workers have added a still larger quota of observations and records so that an enormous mass of rather unrelated data has accumulated. The frequent occurrence of intermediate forms between both species and genera offers many problems to the taxonomist, and the classification of the members of the group presents considerable difficulties.

So far as British desmids are concerned, something of their variety was first rendered accessible through the work of Ralfs which appeared in 1848. More than 50 years later followed the impressive monograph compiled by the Wests, which was published in five of the Ray Society's volumes between 1904 and 1923. Both father and son did not live to see the completion of this great work, and the last volume was prepared for press by Dr. Nellie Carter. The Ray Society monograph gave an immense stimulus to the study of the desmids the world over. The many species and varieties are described with meticulous attention to detail and illustrated by a wealth of clear and accurate figures so that for the first time the diagnostic characters of a large proportion of the commoner desmids became fully accessible to the worker. The unstinted praise that is due in this respect, however, also calls forth a major criticism. I think that there can be no doubt that the Wests overexaggerated the importance of minor detail and thereby to some extent masked more important trends, and the authoritative lead they gave in this respect was followed by most subsequent workers, including myself.

Innumerable species and varieties have been described during the first half of this century, a considerable number differing from earlier established ones only in minor matters of detail. There is, moreover, a widespread lack of balance, many of the newer species differing from the older and from one another to a less degree than do the so-called varieties or forms of other species. There is consequently much difference of opinion, and the synonymy is considerable. In certain species, where the shape or ornamentation are recognized

as subject to appreciable variation, large numbers of variants have been recorded, and nearly every taxonomic list contains descriptions of more or less numerous forms of this kind. There is little evidence, however, that the vast majority of these possess any marked degree of constancy, although it must be recognized that variants, exhibiting comparatively trivial differences and probably representing distinct ecological types, are sometimes remarkably widespread.

To give some idea of the present position I may mention that, of the genus *Cosmarium*, some 1,000 'species' have been described and, if we were to include the varieties, many of which have just as much right to specific rank as some of the species, the total number of entities would probably exceed 2,000. Of *Staurastrum* the equivalent numbers are about 700 and 1,400 respectively. I cite these, the two largest genera, because they are the ones around which the observations I have to make to-day will largely centre. An appreciable number of their species and varieties, as also those of other desmid genera, have only rarely been recorded, many of them only once. Some of these are no doubt geographically-restricted forms, while in other instances the failure to find them again may be due to the fact that the freshwater flora of many parts of the world has so far been but little explored, or sometimes to the description and illustration being so inadequate that the forms in question are difficult or impossible to recognize, as with some of the species described by Turner (1892) from India. Quite frequently, however, I suspect that such species, differing as they often do only in slight respects from previously established ones, have, when found by others, merely been assigned as forms to the better-known species.

When one surveys the numerous described desmids as a whole, it is evident that evolution has taken place along a multiplicity of different lines and that, as in other algal groups, there has been widespread parallel development. The least specialized desmids, exemplified by *Cylindrocystis*, *Penium*, certain species of *Cosmarium*, etc., are rod- or somewhat barrel-shaped forms, with rounded ends and circular in cross-section (fig. 1, B, C; cf. also fig. 2, B, C). Many of these (figs. 1, B, C; 5, A) are not much longer than broad and suggest a derivation from an ancestry with spherical cells (Fritsch, 1933, p. 21); in some in fact the shape does not depart far from the globular (figs. 1, F; 2, C). Such species rarely possess any appreciable ornamentation on their cell-walls and their zygospores, where known, are simple globular structures devoid of any embellishments (figs. 1, F; 7, D). The transverse symmetry, that characterizes the vast majority of desmids, already finds expression in these simple forms in the presence of a single axile chloroplast, with a large central pyrenoid, in each half of the cell (fig. 1, A, C) or semicell, as it is usually called. Only in a few do we find only one chloroplast in the cell, as in *Cosmarium subtilissimum* (West, 1914, p. 1041; fig. 1, B) and occasionally in *C. subtile* (West) Lütkem., a condition which suggests that the paired chloroplasts typical of most of the simpler desmids are perhaps to be regarded as a precocious division-stage.

In many, even of the simpler, desmids the two semicells are separated by a transverse constriction termed the sinus (figs. 1, A, B; 2, C), although this is lacking in a few (e.g. *C. mooreanum* (Arch.) Lütkem., fig. 1, C). In the more specialized forms among the Cosmarieae in the narrower sense* the constriction is often deep (fig. 1, D, E, I, J) so that the two semicells are only linked by a comparatively narrow isthmus, the shape of the sinus affording a taxonomic character which is occasionally of some importance. Deepening constriction in these forms is usually associated with a more or less marked flattening of the cell so that the cross-section comes to be oval or elliptical in outline and the radial longitudinal symmetry of the more primitive desmids is lost (cf. figs. 1, D; 3, e). In certain groups of species among the Cosmarieae

* Viz. *Cosmarium*, *Euastrum*, *Micrasterias*, *Arthrodesmus*, *Xanthidium*, *Staurastrum*.

the transition from forms with a circular to those with an elliptical cross-section can be followed by gradual steps (cf. p. 273). A necessary consequence of the assumption of an elliptical cross-section is that the cell as a whole becomes proportionally shorter, i.e. there is a change in the length-breadth ratio. The flattened cell naturally rests on one of its broader surfaces, exposing what is called the front-view to the observer, while the degree of flattening is recognizable when the cell stands on its end, i.e. is seen in end-view (figs. 1, D ; 3, B, C, e).

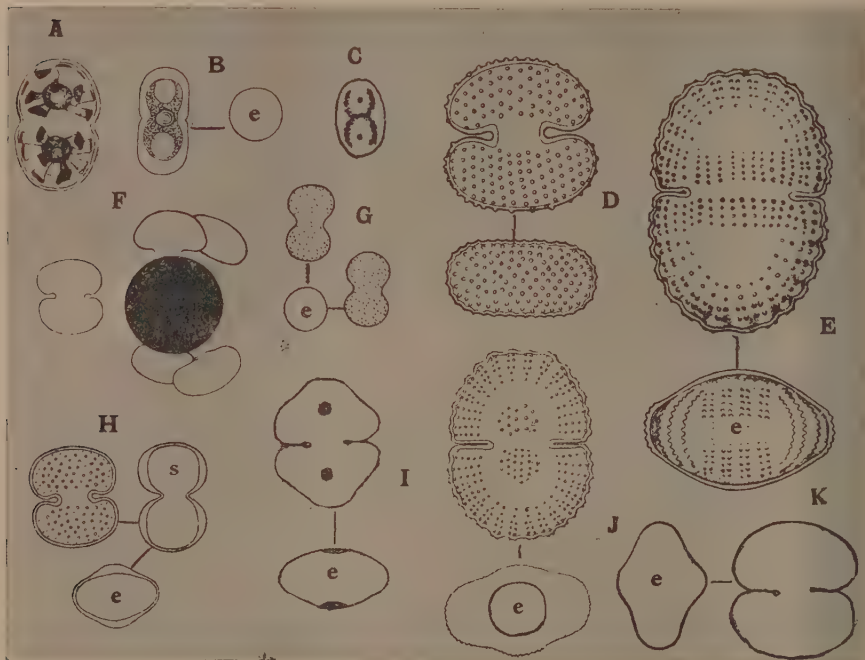


FIG. 1.—Range of shape and ornamentation in Desmids. A, *Cylindrocystis pyramidata* W. & G. S. West (*Cosmarium cylindrocystiforme* G. S. West, 1912, p. 85). B, *Cosmarium subtilissimum* G. S. West. C, *C. mooreanum* (Arch.) Lütkem. D, *C. reniforme* (Ralfs) Arch. var. *compressum* Nordst. (granulate). E, *C. speciosum* Lund. var. *biforme* Nordst. (complex ornamentation). F, *C. melanosporum* Arch. ; zygospore on right. G, *C. moniliforme* Ralfs f. *panduriformis* Heimerl (punctate membrane). H, *C. tumidum* Lund. (scrobiculate membrane). I, *C. luscum* Borge (ocellate). J, *C. subspeciosum* Nordst. (complex ornamentation). K, *C. clepsydra* Nordst., forma. e, end- and s, side-view. (A, F, G after W. & G. S. West ; B after G. S. West ; C, I, K after Borge ; H after Lowe ; D, E, J after Nordstedt). (A, F, G $\times 520$; B $\times 1,000$; D, H $\times 400$; E, J $\times 570$; K $\times 740$; the rest (incl. the zygospore in F) $\times 600$.)

The principal forms of semicells are shown, as seen in front-view, in fig. 2, where their suggested interrelations are indicated. Practically all the more specialized kinds of outlines presented by the *Cosmarium*-cell in front-view are, in one species or another, connected with the rounded type (fig. 2, H, I, M, T) which is no doubt primary. Moreover, the rounded contour is preserved in end- (fig. 3, B, C, e) and side-views (fig. 3, B, L, s) of the majority of even the most highly differentiated species.

The more or less circular or oblong outline of the cell (cf. fig. 2, B) in the less specialized desmids is departed from in many species of *Cosmarium*. Deepening of the constriction, if the sinus remains open, affords moniliform cells (figs. 2, H; 5, I) with almost circular semicells, while, if the sinus be narrow (i.e. linear), semicircular semicells (fig. 2, T) are obtained. Lengthening along the longitudinal axis gives penioid types (fig. 2, D, E) or, if lengthening

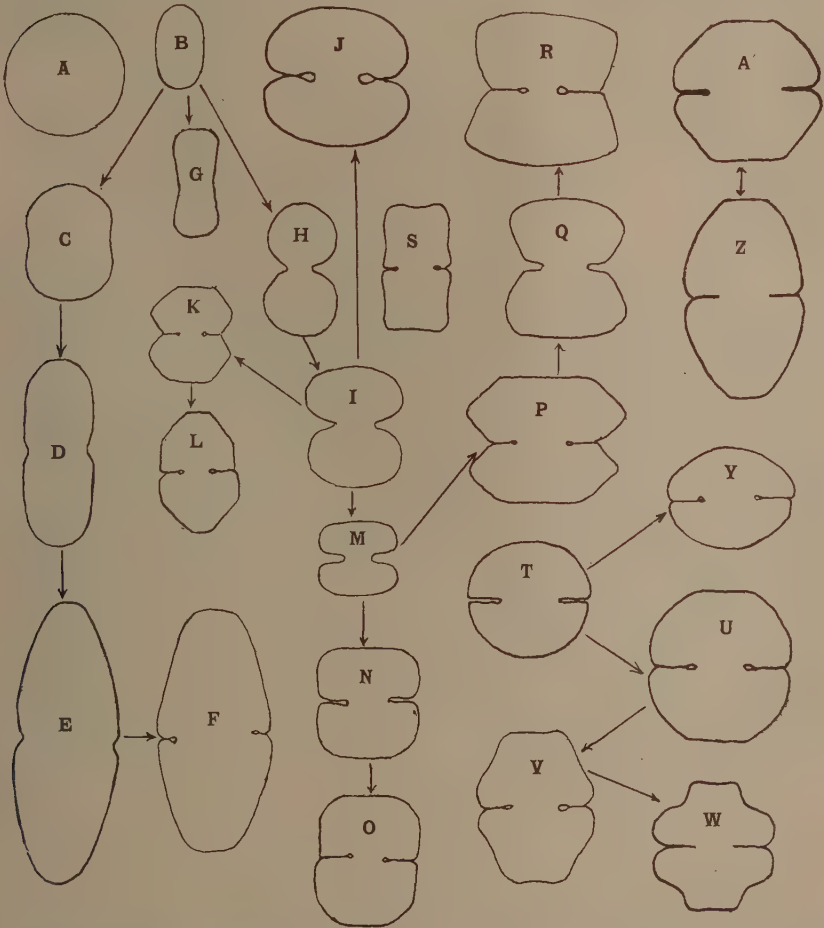


FIG. 2.—Shapes of *Cosmarium*-cells (for F-Z, and A', the designations refer to the semicells). A, possible ancestral form. B, oblong. C, subcircular, constricted. D, E, penioid. F, pyramide. G, obcuneate. H, subcircular. I, M, elliptical. J, reniform. K, hexagonal. L, *granatum*-type (cf. fig. 4, I-U). N, O, transversely subrectangular. P, transversely hexagonal. Q, R, obcuneate. S, subrectangular. T, semicircular (cf. fig. 1, F). U, cosmarioid (cf. fig. 3). V, W, euastroid. Y, dome-shaped. Z, pyramide. A', trapezoid.

be considerable, forms like *Docidium* and *Pleurotaenium*, while broadening of the transverse axis affords types with elliptical semicells (fig. 2, I, M), the latter very common in the species of *Cosmarium* (fig. 8) and *Staurostrum* (fig. 9). Semicells of this and other rounded shapes often merge imperceptibly,

by enlargement of the inner part of the sinus, into such as are reniform (figs. 1, D ; 2, J), or, by flattening of some of the contours into such as appear polygonal (often hexagonal, fig. 2, K, P). The latter, in their turn, readily pass over to semicells which are inversely wedge-shaped or obcuneate (fig. 2, Q), although semicells of this shape can also apparently derive directly from the elliptical or circular form (fig. 2, R).

Flattening of the semicircular type, with increasing convergence of the lateral margins, results in dome-shaped (fig. 2, Y), while lengthening, accompanied by more or less marked flattening of the apex, gives trapezoid (fig. 2, A') and pyramidate (fig. 2, Z) semicells. Comparatively short

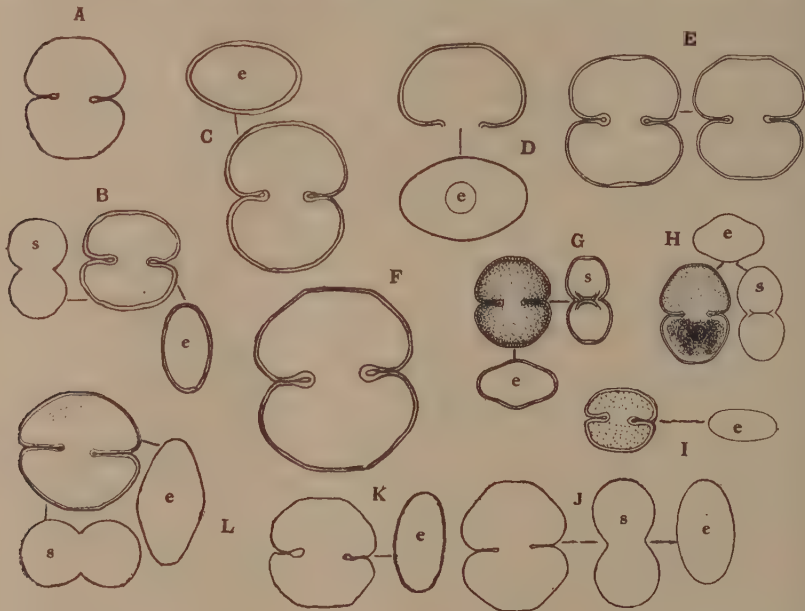


FIG. 3.—*Cosmarium subtumidum* Nordst., as delineated from various regions. A, Britain (W. & G. S. West, 1905) (30–40 × 26–33; ist. 8–11; cr. 17–19). B, Sweden (Borge, 1913) (23–26 × 23–26; ist. 7–9; cr. 13–15). C, Sweden (Borge, 1913) (34–41 × 26–34; ist. 9–12; cr. 18–20). D, Switzerland (Messikommer, 1927). E, United States (Prescott, 1938) (35 × 27; ist. 11–5). F, Newfoundland (Taylor, 1934) (42 × 34; ist. 10). G, Burma (Skuja, 1949) (26 × 23–24; ist. 6–7; cr. 14). H, China (Skuja, 1937) (34–35 × 24–25; ist. 7–8; cr. 19). I–K, var. *klebsii* (Gutw.) W. & G. S. West; I, forma, Irish plankton (W. & G. S. West, 1906) (22–23 × 25–27; ist. 8–9; cr. 11–5); J, Transvaal (Nygaard, 1932) (30 × 24; ist. 7; cr. 14); K, Britain (W. & G. S. West, 1905) (32–41 × 29–35; ist. 7–11; cr. 16–18). L, var. *circulare* Borge, Brazil (Borge, 1903) (28–31 × 28–31; ist. 7–9; cr. 14–16). Measurements in μ . cr. stands for thickness; in most cases decimals have been ignored. e, end- and s, side-view. (A, I, K × 450; F × 625; G × 510; H × 400; the rest × 640.)

pyramidate forms, with markedly convex lateral margins and a more or less clearly flattened apex, are particularly characteristic of many species of *Cosmarium* (fig. 2, U) and may be termed the cosmarioid type. In a considerable number of species, with pyramidate and cosmarioid semicells, the upper parts of the lateral margins are retuse, often markedly so (e.g. *C. protractum* De Bary), in which case the apex of the semicell appears more or less clearly produced (fig. 2, W) so that demarcation from a certain group of species of *Euastrum* becomes difficult (cf. Cedergren, 1932). This

feature is not uncommonly combined with a retuse apex (fig. 2, V), sometimes sufficiently marked to resemble the apical notch of other species of *Euastrum*; such semicells can be described as euastroid. Subrectangular (fig. 2, S) or transversely rectangular (fig. 2, N) semicells, in which the lateral margins are more or less straight and parallel, are not as common as most of the other types. There are comparatively few species of *Cosmarium* that possess semicells of a shape that does not conform to one of the categories I have distinguished, and it is unnecessary to consider them here.

The interrelations of the various types suggested in fig. 2 are in the main based on a comparison of published figures of various commoner desmids which, while agreeing in major essentials, vary somewhat in shape in one direction or the other (fig. 3, A-F; cf. also p. 273). Species with a wide geographical distribution, and there are a considerable number of these, are rarely represented by altogether identical forms in different parts of the world, as is shown by the illustrations that often accompany their citation in taxonomic lists (fig. 3, A-F). These not only commonly indicate an appreciable range of form within the area of distribution of the species, but

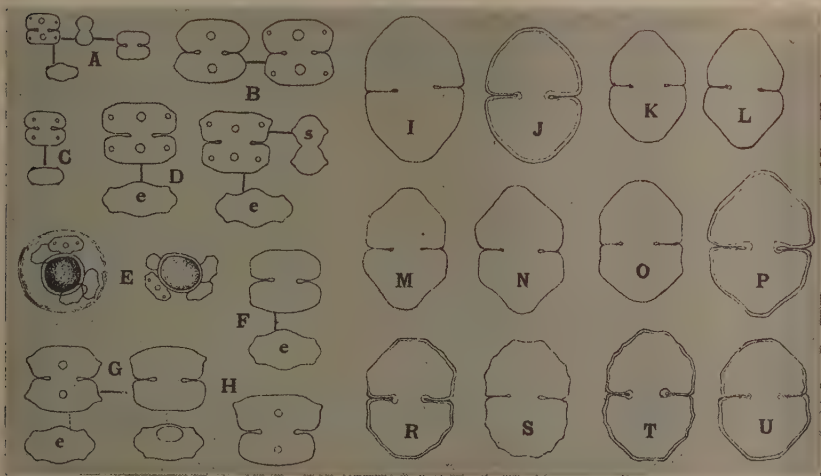


FIG. 4.—A-H, *Cosmarium pygmaeum* Arch. (after W. & G. S. West, 1908, pl. 71, figs. 22-31). I-U, *C. granatum* Bréb. (after Borge, 1921). e, end- and s, side-view. (A, C, E $\times 460$; B, D $\times 885$; F-H $\times 1,100$; the rest $\times 775$.)

sometimes suggest, even on the part of reputable investigators, very diverging conceptions of the fundamental shape of the relevant species, sometimes so much so that it is clear that in their classification reliance has been placed in the main on points of detail (cf. fig. 3, G, H). It would indeed frequently be difficult to justify the inclusion of all the forms thus illustrated within the confines of a single species, in view of the obviously narrow limits maintained for others. There are no doubt a certain number of species in which the characteristics of the front-view tend to vary very considerably in different individuals. This is so, for instance, in *Cosmarium pygmaeum* Arch., where the illustrations (fig. 4, A-H), reproduced from the Wests' monograph, show an appreciable range of form. *C. granatum* Bréb. furnishes another example; all the individuals shown in fig. 4, I-U, taken from Borge's paper (1921) on the algal flora of Lake Tåkern in Sweden, came from the same water. But such are the exceptions to the rule that the form of the cell of most species of desmids is remarkably constant.

In order to be able to evaluate the degree of variability of the desmid cell and to assess its evolutionary importance, as well as to survey the immense number of recorded forms so as to achieve an arrangement of them suitable to display their interrelationships, it is necessary to adopt certain basic criteria as starting points. I have proceeded on the assumption that shape (i.e. form of both front- and end-views) and relative proportions (the length to breadth ratio) afford the best basis for grouping the recorded forms of the desmids under consideration and that all other characteristics are of secondary importance. This depends on the recognition of the fact that, despite the minor fluctuations previously discussed, shape and the general length to breadth ratio are astonishingly constant in whole series of species, even though actual dimensions, as well as other features, may vary to a very considerable extent. On this basis it is possible to arrange the bulk of the recorded forms of *Cosmarium*, *Staurastrum* and other Cosmarieae in what I will call species-groups (cf. e.g. fig. 7), some of them very clearly marked, others not so sharply defined.

In every such species-group we commence with species in which the outline is even (sometimes undulate (fig. 4, S, T) or crenate) and the membrane smooth (fig. 3, A-E). In other members of the group it is ornamented in one way or another, the ornamentation taking the form of scrobiculi (cf. figs. 1, H; 8, U), that is, usually rather shallow rounded depressions of the membrane, or consisting of variously shaped granules, warts or spines (figs. 1, D; 8, R, W); sometimes, but more rarely, several types are combined. The ornamentation is often uniformly distributed over most of the wall (figs. 1, D; 8, U; 9, L) and not uncommonly arranged according to a definite pattern (quincuncially or in vertical and horizontal series), but the region of the isthmus is commonly smooth, and in a certain number of species it is confined to a comparatively small part of the wall (fig. 9, G). A good deal of stress in desmid description is often laid on the presence or absence of small dots called punctae (fig. 1, G), but this appears to be a character of questionable value. These punctae are actually minute pores in the membrane, through which mucilage-exudation takes place; they are no doubt present in most, if not in all, desmids, but become readily conspicuous, especially if the cell be stained, only when marked excretion of mucilage is occurring. Their mode of arrangement on the wall, especially in the larger species, often affords an important characteristic. At times when the exuded threads of mucilage are particularly firm, they may appear as small projecting bristles, and in the description of some species these have been confused with small spines. One may even suspect that some of the finer granulations of the wall, recorded in various species, may be nothing else than the consolidated mucilage excreted from the pores.

In many desmids showing the diverse shapes and ornamentations just described the outline of the cross-section, as seen in the end- (sometimes called the vertical) view, remains a simple ellipse. There is, however, a frequent tendency for the middle region of the face of the semicell to undergo special thickening of the wall (fig. 1, H) or, more commonly, to exhibit a more or less considerable inflation (a so-called tumour, figs. 1, K; 3, G, H; 5, E), both of them features which are particularly easy to recognize in the end-view (*e*) and which are marks of specialization. When there is but a thickening of the wall, it is sometimes occupied by a single prominent scrobiculation (ocellus, fig. 1, I), one of the many special developments that reappears in various evolutionary series among these desmids. In what I think are to be regarded as the most highly specialized members of the genus *Cosmarium* the central thickening or protuberance of the semicell exhibits a special ornamentation different from that found on the rest of the wall and usually separated from it by a clear space (figs. 1, E, J; 5, C). This feature is also seen in the often complexly ornamented forms grouped in the genus *Xanthidium*, as well as in most species

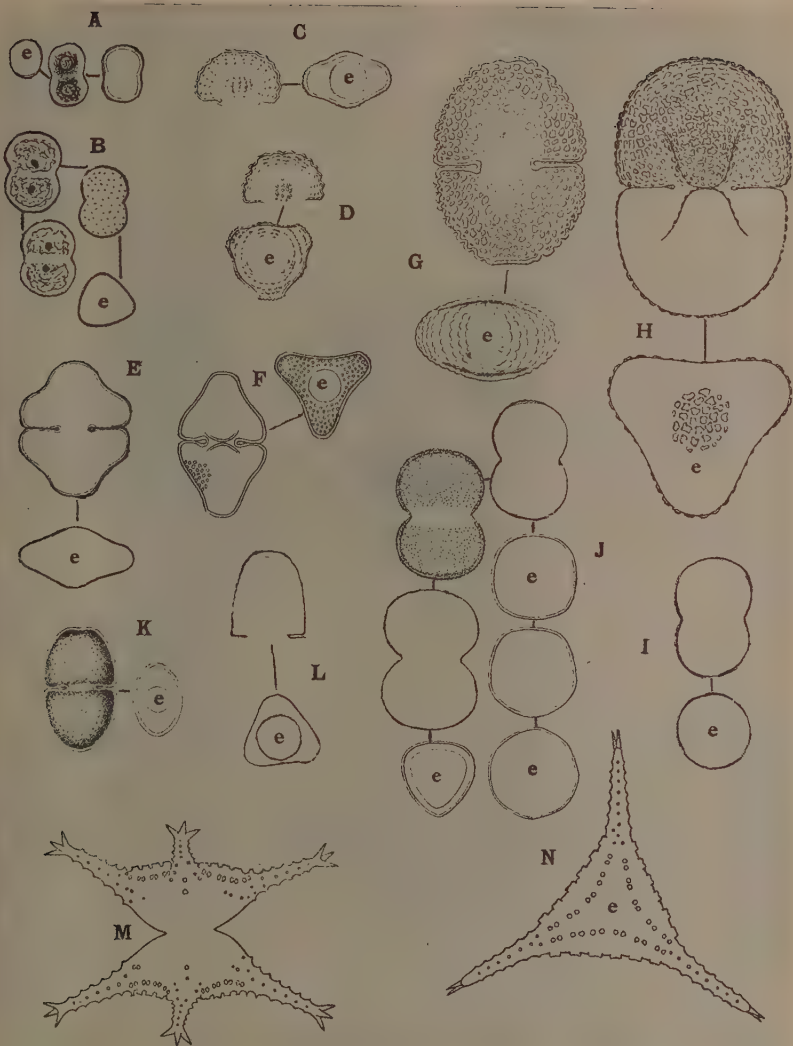


FIG. 5.—*Cosmarium* and *Staurostrum*. A, *C. pseudarctium* Nordst. (after W. West, 1892). B, *C. pseudarctium* var. *trigonum* Borge (after Borge, 1923). C, *C. subcrenatum* Hantzsch (after Nordstedt, 1875). D, *C. subcrenatum* var. *triquetrum* Nordst. (after Nordstedt, 1875). E, *C. aequale* Turn. (after Turner, 1892). F, *Staurostrum trihedrale* Wolle (after W. & G. S. West, 1896). G, *Cosm. ochthodes* Nordst. (after Nordstedt, 1875). H, the same, probable triquetrous form (after Dick, 1919)*. I, *Cosm. globosum* Bulnh. (after Krieger, 1936). J, *Staurostrum subsphaericum* Nordst. (after Nordstedt, 1875). K, *Cosm. pseudopyramidatum* Lund. (after Lundell, 1871). L, *Staurostrum cosmarioides* Nordst. (after Nordstedt, 1869). M, N, *Staurostrum anatinum* Cooke and Wills (after W. & G. S. West). e, end-view. (B $\times 580$; C, D $\times 550$; E $\times 480$; G, J–L $\times 380$; H $\times 440$; the rest $\times 500$.)

* This was described as a doubtful form of *Staurostrum alpicolum* Schmidle by Dick (1919. p. 253), but is no doubt to be assigned to *Cosm. ochthodes*.

of *Euastrum*, some of which bear a number (always uneven) of such tumours on the face of the semicell.

A very significant variation in the shape of the *Cosmarium*-semicell is the assumption of a triangular outline in cross-section (fig. 5). The majority of such variants have been described as species of *Staurastrum*, because in them the triangular cross-section is the rule. But, in quite a large number of species of *Cosmarium*, as well as in a few of those belonging to related genera (*Euastrum*, *Xanthidium*, *Micrasterias*), in all of which the end-view usually presents an elliptical two-sided outline, triangular varieties have been described under the name of var. *trigona* or var. *triquetra* (cf. fig. 5, B, D, H). Except for this particular feature, these varieties, especially in the characteristics of the front-view, are essentially like the typical forms of the species in question, in which the end-view is two-sided (fig. 5, A, C, G). The position is, however, quite illogical, since for many of the simpler trigonal species of *Staurastrum* comparable *Cosmarium*-species are known (cf. fig. 5, E and F; I and J; K and L) which, though perhaps not always altogether identical in front-view, nevertheless bear much the same relation to the *Staurastrum*-species as do the trigonal forms of many species of *Cosmarium* to the non-trigonal forms of the same species. Similarly there are a number of species of *Staurastrum* with 4-, 5- or more-angled end-views, for which it is possible to find almost exact replicas among the species of *Cosmarium* (cf. fig. 5, I, J).

It would probably be most appropriate to group together all the *Cosmarium*-like forms, in which the end-view is 3- or more-sided with non-produced angles, under one common generic heading, for which the name *Cosmostaurastrum* may be suggested. Its only distinctive feature, by contrast to *Cosmarium*, but that perhaps a rather fundamental one, would lie in the shape of the cross-section of the semicells, and many of its species would have close parallels among those of *Cosmarium*.

The two-sided end-view that is distinctive of so many species of the last-named genus may either be oval with broadly rounded poles and only slightly convex sides (cf. figs. 1, D; 8, e), or the poles may run to a point (fig. 5, E, e), or even be slightly produced. This tendency towards a prolongation of the poles is met with in many species of *Staurastrum* and especially in those which play a conspicuous part in freshwater plankton (fig. 5, M, N). It is for forms of this kind that the genus *Staurastrum* was first established (Meyen, 1828) and to which it is now suggested it might best be confined. The appearance, both in front- and end-views, is for the most part markedly different from that of the species grouped in *Cosmarium* or *Cosmostaurastrum*, although it would be difficult to draw any very hard and fast distinctions between the two sets of forms. While in many species the production of the cell-body into long arms is very obvious (fig. 5, M, N), there are other species in which the arms are comparatively short or subject to appreciable variation in length (e.g. *S. brachiatum* Ralfs, cf. West, 1899, p. 392).

Although the species of *Staurastrum*, regarding the genus in the restricted sense just suggested, often have biradiate semicells, they are commonly tri- or quadriradiate and some even exhibit a larger number of rays when seen in end-view (fig. 9, N, e). While the trigonal or triradiate form is the rule in many species of *Cosmostaurastrum* and *Staurastrum* respectively, and is indeed often the only one known, others and especially those of *Staurastrum* in the restricted sense, often exhibit considerable variation in this respect and present us with 2-, 3-, or more-rayed forms without any other appreciable change in character. They exemplify the extreme plasticity of the desmid-cell and suggest that, once the tendency for protrusion of the semicell has developed, it may take place at a variable number of points. Although the semicells of an individual are usually alike in this respect, specimens are occasionally found in which the number of rays differs on the two semicells.

I have already referred to the fact that there is good reason to believe that the desmids are derived from an ancestry with globose or perhaps somewhat oblong cells, with a circular cross-section and radial symmetry. This radial symmetry has been preserved in various otherwise specialized genera like *Closterium*, *Tetmemorus* and *Pleurotaenium*, with which we are not concerned here. Similarly, there is a considerable number of species of *Cosmarium* (figs. 1, B ; 7) still retaining the radial longitudinal symmetry, while some of the species to be grouped in *Cosmostaurastrum* have an almost circular end-view (fig. 5, J), with only faintly indicated angles, which in such forms are commonly rather numerous. It might therefore be feasible to assume that, in the radially symmetrical ancestor, there arose a tendency for protrusion of the cell along certain radii of the cross-section, these points of protrusion being at first rather numerous and symmetrically disposed around the periphery, and that by a gradual process of reduction the number of protrusions became lessened until only 4, 3, or 2 remained. In other words, the flattened *Cosmarium* type or the triangular or triradiate staurastroid types would be the culmination of a series of reduction in the number of planes of longitudinal symmetry. This, if I understand him rightly, is the point of view put forward by Teiling (1950, p. 318) in a most instructive paper in which he discusses the symmetry-relations of desmids.

There are, however, in my opinion certain considerations that speak against a complete acceptance of his point of view, so far as the bulk of the species of *Cosmarium*, *Cosmostaurastrum* and *Staurastrum* are concerned. It is difficult to find any satisfactory evidence for the derivation of the flattened *Cosmarium* type with a two-sided end-view from an ancestry having an end-view with three or more sides. On the other hand, in certain species-groups there is, as already mentioned, a gradation from forms with a circular to forms with an elliptical cross-section. The bulk of the species of *Cosmarium* with a circular or subcircular end-view possess simple outlines and are unornamented or exhibit simple ornamentation only (cf. fig. 7, A-S) ; where the zygospores are known, they are for the most part spherical and with a smooth wall devoid of appendages. It is among the markedly flattened species, and especially among those with a tumour on the face of the semicell, that we find a large number of species with complex ornamentation and zygospores of an elaborate type (cf. Fritsch, 1933, pp. 24, 30). A progressive elaboration of the flattened type of *Cosmarium*-cell thus seems to have occurred.

Among the species of *Staurastrum* sens. str., those which customarily possess three or more arms are in no way less specialized in other characters than those which are usually biradiate. Flattening of the *Cosmarium*-cell probably took place at a comparatively early stage in the evolution of these desmids, and this type was subsequently elaborated in the various ways previously discussed. Although those species of *Cosmostaurastrum* and *Staurastrum*, which show a multiradiate symmetry in their end-views, may quite possibly have arisen direct from forms with circular end-views, the bulk (and especially the triangular or triradiate forms) almost certainly arose from the flattened *Cosmarium* type before it had evolved very far. This is shown by the fact that various species of *Cosmostaurastrum* differ only in minor respects, apart from their triangular end-view, from species of *Cosmarium* in which flattening is a fixed character.

There is one other significant development that appears to have occurred in diverse evolutionary series among these desmids. When one brings together groups of species that show essentially the same shape of cell and the same length to breadth ratio, whether they be smooth or ornamented in one way or another, a certain number are usually found to be distinguished by exceptional size. It is not a case of size-variation within certain rather wide limits, such as is found in some desmid-species ; the forms in question are usually strikingly

different in dimensions from others of their group, not uncommonly being two or more times as large, though preserving the length-breadth ratio characteristic of it. They give altogether the impression of being giant forms which have arisen by a sudden mutation. Hand in hand with the assumption of the large size there often goes a change in internal structure.

In the majority of the smaller desmids we have been discussing each semicell usually contains either one (fig. 6, A, B) or two (fig. 6, C, D) axile chloroplasts, each mostly with a large central pyrenoid. The structure of these chloroplasts is frequently complex, with a number of rather regularly disposed plate-like processes which, especially in the bigger forms, tend to spread out at their periphery into more or less clearly marked superficial bands (fig. 6, B). There is considerable variety of structure which has been disclosed by the investigations of Dr. Carter (1920), but with which it is impossible to deal to-day. The giant forms, to which reference has just been made, almost

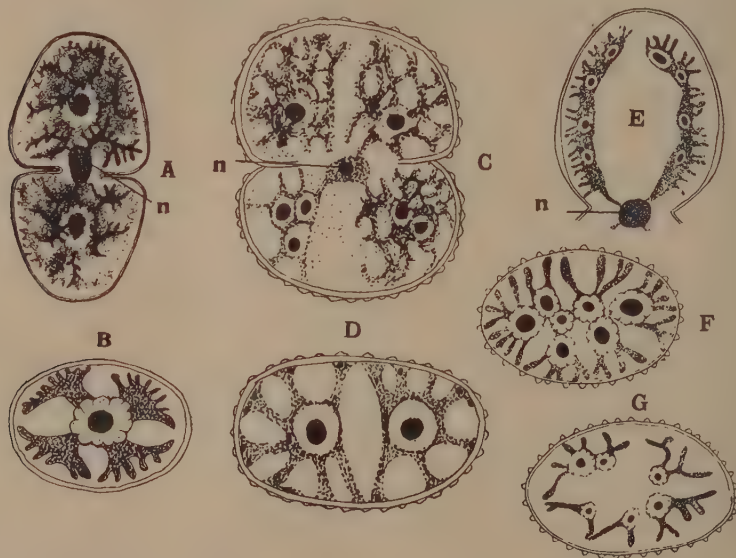


FIG. 6.—Chloroplasts of Desmids (all after Carter, 1920). A, B, *Cosmarium pseudopyramidatum* Lund. (one axile chloroplast in each semicell). C, D, *C. reniforme* (Ralfs) Arch. (two axile chloroplasts in each semicell). E, *C. ovale* Ralfs, optical section (parietal chloroplasts). F, G, *C. brebissonii* Menegh. (transition to parietal chloroplasts). B, D, F, G are transverse sections. n, nucleus. (A, F, G $\times 500$; H-D $\times 650$; E $\times 300$.)

invariably contrast with their smaller relatives in possessing a number of parietal band-shaped chloroplasts, with scattered pyrenoids, in each semicell (figs. 6, E; 7, Z; 8, J). The researches of Lütkenmüller (1893) and Carter (1920) have, I think, made it clear that this condition is secondary and that the parietal bands are the equivalents of the peripheral enlargements of axile chloroplasts in which the central portions have been suppressed (cf. fig. 6, F, G). The change is one which apparently usually goes hand in hand with the great increase in the volume of the cell.

In a polyphyletic assemblage like that of the desmids, in which evolution appears to have exhausted almost all possibilities, and homoplastic development is so widespread, generic distinction is bound to be arbitrary and highly artificial and to fail altogether among the borderline species which are transitional in

character. There is, however, no other way of classifying the huge number of forms involved. I am of the opinion that a true assessment of affinities can only be undertaken when these artificial genera are ignored and the recorded forms of desmids are assembled on the basis of their fundamental cell-shape. In constructing such species-groups existing varieties will in part acquire a new status and be segregated from the species to which they are at present referred. The species-groups are an expression of the multiplicity of evolutionary series among the desmids. They transcend present generic limits and afford examples of parallelism in development unsurpassed in any other series of the algae. Their value lies in placing comparable forms side by side and in displaying what are probably the true interrelationships of their members. The ultimate purpose, however, is to survey the mass of accumulated records from the point of view of geographical distribution.

The opinion has often been expressed that the desmids will provide an interesting study of geographical distribution within a natural group and that they may furnish criteria on former land-connections. They are almost without exception inhabitants of freshwaters, only a few of the relatively unspecialized species occurring on terrestrial substrata. They are to be found in suitable habitats the world over. The only region in which they are apparently very scantily represented is the Antarctic. Unlike a large proportion of the other freshwater algae, only a fraction—albeit a fairly big one—of their species is ubiquitous. Quite a considerable number, which possess distinctive characteristics and have been well described, are restricted to certain regions, although so large a part of the freshwaters of the world are yet unexplored that we must step warily. Even if we exercise due caution, however, it is safe to say that certain species appear to have a limited area of distribution and that many of the most striking species appear to be thus restricted. Most of the species listed by G. S. West (1907, p. 82; 1914, p. 1015; cf. also West & West, 1907, p. 176) as Indo-Malayan, Australasian, Tropical African, and South American, still, after 30–40 years, stand unchallenged as endemics in these regions, although a few have had their area of distribution in the Southern Hemisphere widened as a result of subsequent researches. The number of such geographically limited species could, moreover, be somewhat increased nowadays. The justification for regarding such species as endemics, especially characteristic of the regions from which they were first described, is strengthened when they have been recorded two or more times, sometimes at long intervals, from the same area.

The normal, and often very prolific, method of reproduction of the desmid is by cell-division, while sexual reproduction, usually involving the fusion of the protoplasts of two individuals and resulting in the formation of a zygospore, the only known resting stage in the life-cycle, is resorted to only at certain times. Meiosis takes place during the germination of the zygospore, with the formation of two, or more rarely four, individuals. Although gene-mutations need not be ruled out, it is probably the syngamy and subsequent meiosis that occurs in relation to the sexual process that affords most scope for the evolution of new and distinctive types. Except in comparatively few desmids, however, zygospores are rarely formed, and there are quite a large number of widely distributed species in which they have only been observed once or twice or even never yet been described.

Wind-distribution may play some rôle in the spread of the drought-resisting zygospores within a limited area, but the usual agents, both for short- and long-distance dispersal, are almost certainly birds. The half-dried mud that adheres to the feet of wading birds may harbour either spores or vegetative individuals, while the latter may be caught up amid the plumage of bathing birds. Successful dispersal of vegetative individuals by these means will depend on the interval elapsing before a new habitat is reached,

MONILIFORME--GROUP

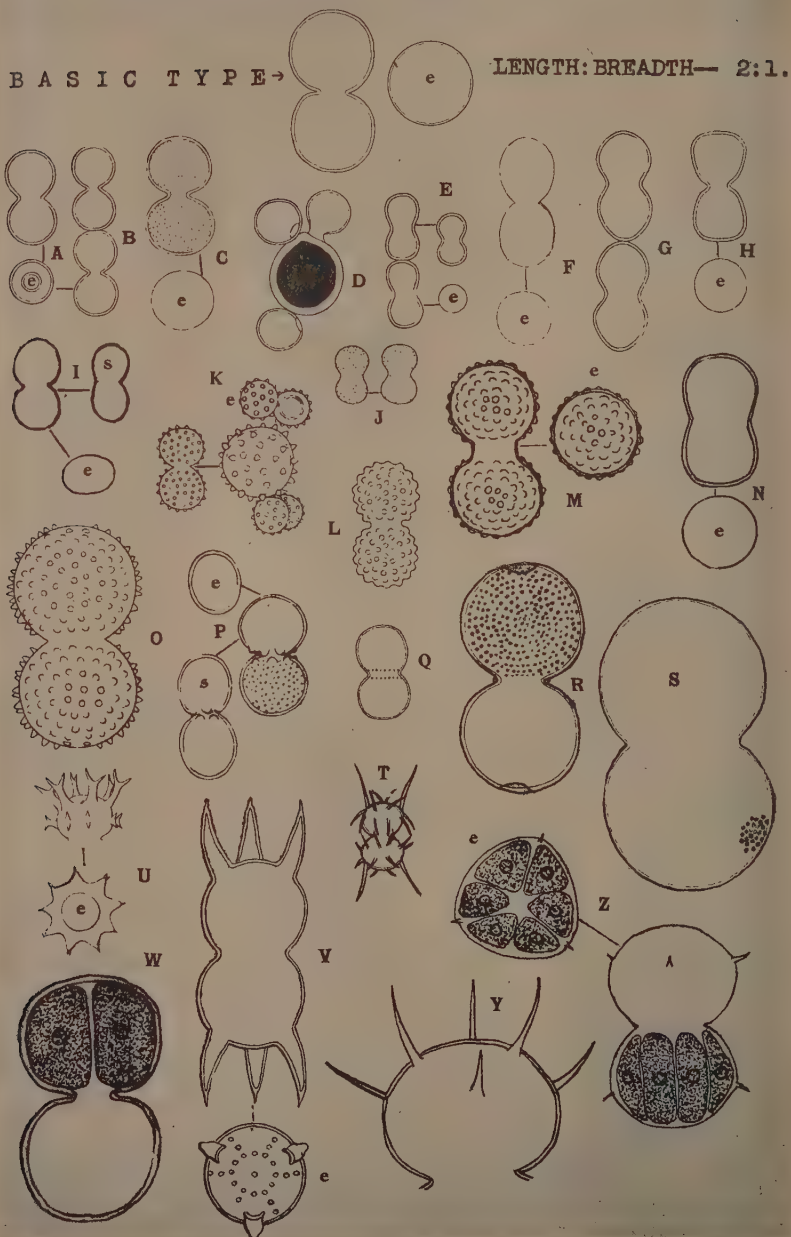


FIG. 7.—The *moniliforme* group. For description, see table I, p. 271. *e*, end-, and *s*, side-view. (A, B, D, I, K, L, O $\times 350$; C, G, H, J, Z $\times 450$; E, N, Q, S, T $\times 430$; F, U $\times 500$; M $\times 670$; P $\times 520$; R $\times 230$; V $\times 680$.)

TABLE I.—Moniliforme-Group.

Basic Type : *Cosmarium moniliforme* (Turp.) Ralfs (after Taylor, 1934). Semicells subcircular ; constriction deep ; sinus open, acute-angled ; end-view circular or subcircular ; one chloroplast per semicell.

Fig.	Species	Source of fig.	Length ¹ (μ)	Breadth (μ)	Isthmus (μ)	Geographical distribution	Notes
7, A, B	<i>C. moniliforme</i> (Turp.) Ralfs	Ralfs, 1943	21-33	11-20	4-9	World-wide	Zygosp. (fig. 7, D) globose, smooth
7, C	<i>C. moniliforme</i> f. <i>punctata</i> Lagerh.	W. & G. S. West, 1908	24-43	14-25	3.5-7	Probably world-wide	See p. 264
7, E, J	<i>C. moniliforme</i> f. <i>panduriformis</i> Heimerl	W. & G. S. West, 1908, Heimerl, 1891	17-25	10-15	6-10	World-wide (not so far recorded from S. America and Australia)	Less deeply constricted
7, F	<i>C. moniliforme</i> f. <i>elongata</i> W. & G. S. West	W. & G. S. West, 1897	38-42	17-20	4-7	Ireland and U.S.A.	Semicells longitudinally elliptical
7, G	<i>C. moniliforme</i> var. <i>limbatum</i> W. & G. S. West	W. & G. S. West, 1908	37-52	19-27	12-15	Probably world-wide	Apex of semicell produced ; less deeply constricted
7, H	<i>C. moniliforme</i> var. <i>subpyriforme</i> W. & G. S. West	W. & G. S. West, 1908	40	20	7-7	Probably world-wide (not so far recorded from S. Amer. and Austr.)	Semicells obcuneate, atypical
7, I	<i>C. moniliforme</i> f. <i>elliptica</i> Lagerh.	Lagerhelm, 1885	40	25	12-15	America, Australia, Indonesia	End-view oval
7, K	<i>C. orbiculatum</i> Ralfs	Ralfs, 1848 ; W. & G. S. West, 1908	35-38	18-20	6.5-8	Northern Hemisphere	Membrane granulate ; zygospore with conical warts
7, L	<i>C. orbiculatum</i> f. <i>major</i> W. & G. S. West	Ralfs, 1848 ; W. & G. S. West, 1908	55	23	12.5	Probably the same	
7, M	<i>C. bisphaericum</i> Printz	Printz, 1915	45-47	24-25	11	Europe and Asia	Sinus elongate
7, P	<i>C. basituberculatum</i> Borge	Borge, 1918	35-38	20-21	7-7.5	Brazil	Ring of tubercles at base of semicell ; end-view oval
7, Q	<i>C. basilecorum</i> (Turner)	Turner, 1892	34	18	11	India	Only doubtfully distinct from <i>C. moniliforme</i>
7, N	<i>C. viride</i> (Corda) Josh.	Krieger, 1936	41-55	20-33	14-22	Probably world-wide	Semicells obcuneate, atypical
7, W	<i>C. meyeri</i> Schmüde	Schmüde, 1901	63	36	?	Brazil	Chloroplasts stated to be parietal
7, O	<i>C. praegrande</i> Lund.	Lundell, 1871	97-104	56-61	23-24	Northern Hemisphere	Giant granulate type, with parietal chloroplasts
7, S	<i>C. schomburgkii</i> Borge	Borge, 1899	119-120	67-73	44	British Guiana, Brazil	Membrane punctate (or scrobiculate ?)
7, R	<i>C. patelliforme</i> Borge	Borge, 1903	143-145	76-78	30-31	Brazil	Scrobiculate ; apex of semic. with a concave depression
7, T	<i>Staur. tentaculiferum</i> Borge	Borge, 1899	27-29	17-18	8	British Guiana	End-view rounded-triangular
7, U	<i>S. inaequale</i> Nordst.	Nordstedt, 1877	24 (sine proc.)	18	11.5	Brazil	End-view 9-angled
7, V	<i>S. subunguiferum</i> Fritsch & Rich	Fritsch & Rich, 1937	40-44 (sine proc.)	24-23	13-17	Central and South Africa	End-view circular, with three evenly disposed processes
7, Z	<i>S. ceratophorum</i> Nordst.	Grönblad, 1944	127-143 (99) ²	74-83 (72) ²	25-29	Brazil	(Chloroplasts parietal)
7, Y	<i>S. ceratophorum</i> var. <i>duplicatum</i> Borge	Borge, 1925	77-80 (103) ³	49-53 (64) ³	23-26	South America	Spines longer, with a second apical group of three

¹ In most instances decimals have been ignored.

² The dimensions in brackets are those given by Grönblad (1944).

and small species, that present no large surface for evaporation, will more readily survive the exposure entailed than larger ones, although there may well be differences in the capacities of different species to resist desiccation; the presence or absence of enveloping mucilage may be a decisive factor. Various authorities have emphasized the importance of migratory birds in dispersal of desmids over long distances (Bohlin, 1901, p. 31; Boergesen, 1901, p. 201; Strøm, 1926, p. 44). Bohlin (1901, p. 32) drew attention to the fact that 50% of the species recorded by him for the Azores were also found in the Faeroes and ascribed this to the agency of birds of passage (cf. also Bourrelly & Manguin, 1946).

Unfortunately the agency of birds is largely conjectural and actual carriage remains to be proved. It is little likely that such dispersal would often be successful over wide ocean stretches, such as separate the Antarctic land-masses from the contiguous parts of other continents, while deserts and extensive mountain-chains would probably form equally insurmountable barriers to desmid distribution. Strøm (1924, p. 141) points out that dry limestone districts might equally well form barriers, since few desmids thrive in calcareous waters. There would, therefore, be nothing surprising in the existence of specific Indo-Malayan, Tropical African and Australasian endemics among desmids. How far human agency, by the introduction of freshwater fish and other aquatic animals or of exotic aquatic plants, may play a part in bringing about a rapid transference to regions which might otherwise be inaccessible, is at present unknown. When I examined the algal flora of the artificial basins at Kew at the beginning of the century (Fritsch, 1906), I found only British species of desmids. Some of the species found in tropical or subtropical waters may not find conditions in the temperate zones suitable for existence.

Although a limited number of desmids conjugate with considerable regularity at the appropriate season of the year, the environmental factors requisite for the onset of sexual reproduction in the majority seem only very occasionally to be realized. These special conditions apparently occur most readily in small or comparatively shallow bodies of water in which considerable numbers of species, both widespread ones and others of more limited distribution, are occasionally found in process of conjugation. Thus, Rich (1935) found in a single collection (3 July) from a Transvaal pan, 68 species of desmids, 26 of which showed zygosporangium-formation, while another such pan examined at intervals over a period of years (Fritsch & Rich, 1937) furnished 140 species of desmids, 25 of them with zygosporangia. Although such instances are only rarely observed, this is perhaps due to the natural limits set on the collecting zeal of the student, and they need not be as infrequent as the records seem to imply. Subsequent drought, causing partial or complete drying up of the water, will expose the sediments containing the zygosporangia and admit of the operation of the agents of distribution (wind, birds) already discussed.

Most variety may be expected in those species-groups in which the members resort to sexual reproduction comparatively frequently, although on this matter it is difficult to get satisfactory data, since formation of zygosporangia is by no means always mentioned in floristic surveys. We have to be content with the knowledge that a species can form such spores and that they have been observed in various parts of its area of distribution. When this is so, it is perhaps justifiable to assume that sexual reproduction in the species is not too infrequent and that it has afforded the means for variation. Every species-group includes one or more species known to form occasional zygosporangia and enjoying a wide distribution over the surface of the earth, as well as more or less numerous striking and easily recognized species which are distinctive of certain regions and have never yet been met with in those areas of the world, like many parts of Europe and North America, which may be said to be comparatively well explored. It may be long before it can be said decisively

which of these are true endemics, but meanwhile the assembly of comparable species into groups should help to illuminate the problems of geographical distribution and, in particular, to indicate probable regions of major evolution of new types, that is to say, centres from which dispersal might be effected.

In conclusion I will illustrate the matters to which I have referred by discussing in outline two such species-groups. The first of these is the *moniliforme*-group (cf. also table I) in which the basic type is *C. moniliforme* (Turp.) Ralfs (fig. 7, A-C), which has been found all over the world and probably forms zygospores (fig. 7, D) fairly readily. While the type itself is extremely uniform in its characteristics, the diverse forms and varieties (fig. 7, E-J) that, by practically universal consent, are assigned to it, show a considerable range of shape. Particular attention may be directed to the var. *subpyriforme* (fig. 7, H), which in the distinctive obcuneate shape of the semicells might almost be regarded as the starting-point of another species-group, including *Cosmarium viride* (Corda) Josh. (fig. 7, N). In the f. *elliptica* of Lagerheim (1885) the circular end-view is replaced by an oval one (fig. 7, I; cf. *C. contractum* Kirchn. var. *rotundatum* Borge (1925) which is possibly identical with Lagerheim's form), illustrating the ready passage from one to the other to which I have previously referred. The formae *panduriformis* Heimerl (fig. 7, E, J) and *elongata* W. & G. S. West (fig. 7, F) exhibit minor modifications in other directions and complete the picture of an appreciable range of variation of the central type.

Quite comparable to *C. moniliforme*, except for the uniform granulation of the wall, are *C. orbiculatum* Ralfs (fig. 7, K) and *C. praegrande* Lund. (fig. 7, O), the latter possessing parietal chloroplasts and being about twice the size of the largest known forms (f. *major* W. & G. S. West, fig. 7, L) of *C. orbiculatum*; both species, though widely distributed, are confined to the Northern Hemisphere. It may be noted that the zygospore of *C. orbiculatum* (fig. 7, K) is also more elaborate than that of *C. moniliforme*. *C. bisphaericum* Printz (fig. 7, M), only known from Europe and Asia, differs essentially only in its sinus from the other granulate species of the group. Other species of large dimensions belonging to the *moniliforme*-group are so far only recorded from South America, viz. *C. schomburgkii* Borge (fig. 7, S) and *C. patelliforme* Borge (fig. 7, R), both of which are larger than *C. praegrande*. The structure of their chloroplasts is not known, but another, though appreciably smaller, Brazilian species, *C. meyeri* Schmidle (fig. 7, W), has parietal chloroplasts. Species retaining the dimensions of a *C. moniliforme*, but showing diverse other modifications are *C. basituberculatum* Borge (fig. 7, P) from Brazil and *C. basidecorum* Turn. (fig. 7, Q) from India.

Species to be assigned to *Cosmostaurastrum* that belong to this group are the comparatively small *Staurastrum tentaculiferum* Borge (fig. 7, T) and *S. inaequale* Nordst. (fig. 7, U) from Brazil, as well as the somewhat bigger *S. subunguiferum* Fritsch & Rich from Central and South Africa, all three with end-views that do not depart far from the circular of the basic type. The much larger *S. ceratophorum* Nordst. (fig. 7, Z), another South American species, has parietal chloroplasts and a definitely triangular end-view.

It would appear that in this species-group the smooth types are widely distributed (possibly all world-wide), while the granulate forms (fig. 7, K-M, O) are confined to the Northern Hemisphere. Other kinds of elaborations (fig. 7, P-Z) are almost entirely restricted to the Southern Hemisphere, the chief area of emergence of new types being seemingly South America.

The second example to which I will refer is what I call the *ellipsoideum-contractum*-group (figs. 8, 9; cf. also table II), which is possibly connected to that just discussed by way of the f. *elliptica* (fig. 7, I) of *C. moniliforme*. The basic type seems to be *C. ellipsoideum* Elfving (fig. 8, top), which has usually been regarded as a variety of *C. contractum* Kirchn. (fig. 8, F), but

ELLIPSOIDEUM--CONTRACTUM--GROUP

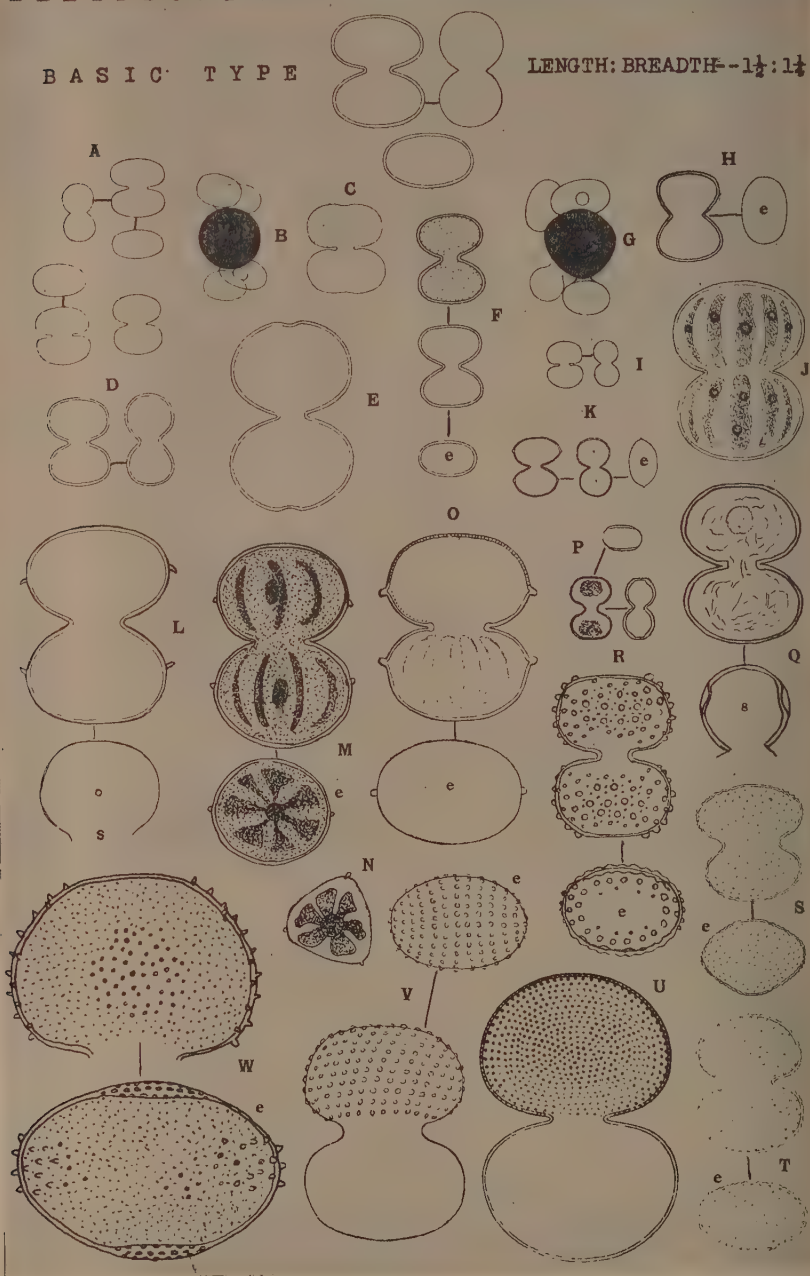


FIG. 8.—The *ellipsoideum-contractum*-group (*Cismarium*-forms). For description, see table II. *e*, end-, and *s*, side-view: (Basic type, A, C, E, F (top figure), I, J, L, N, R–U, W $\times 400$; B, D, F (two lower figures), G $\times 320$; H, Q $\times 550$; K $\times 240$; M $\times 470$; O $\times 520$; P $\times 280$.)

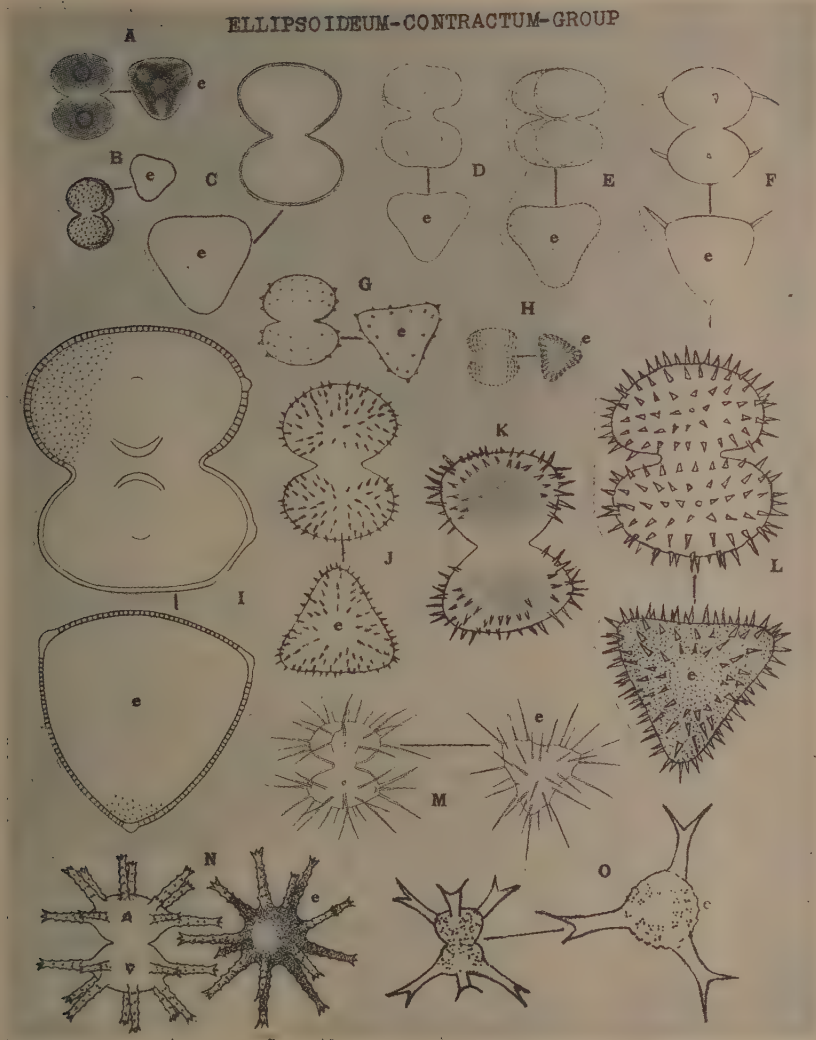


FIG. 9.—The *ellipsoideum-contractum*-group (staurostroid forms). For description, see table II. *e*, end-view. (A $\times 210$; B $\times 390$; C, I $\times 300$; D, E, H, O (front-view) $\times 440$; F, N $\times 250$; G, L $\times 500$; J, K $\times 350$; M $\times 200$; O (end-view) $\times 750$.)

TABLE II.—Ellipsoideum-Contractum-Group.

Basic Type: *Cosmarium ellipsoideum* Elfving (after Elfving) (31·51 × 24·42: ist. 7·12 μ). Semicells in front-view elliptic with rounded convex lateral margins; constriction deep sinus open, usually acute-angled, but tenting (towards parallel edges in some forms; end-view oval, with rounded poles and slightly convex sides; one chloroplast per semicell. Zygosporc globose (fig. 8, B, after Lütkenmüller).

Fig.	Species	Source of fig.	Length ¹ (μ)	Breadth ¹ (μ)	Isthmus ¹ (μ)	Geographical distribution	Notes
8, A	<i>C. ellipsoideum</i> Elfv. var. <i>minutum</i> (Delp.) W. & G. S. West	W. & G. S. West, 1905	22-24	18-20	4-8	Probably world-wide	Small form
8, C	<i>C. ellipsoideum</i> f. <i>retusa</i> W. & G. S. West	W. & G. S. West, 1905	32	27-5	5-5	Ireland, but probably much more wide-spread (China; Jac, 1949)	Apex retuse
8, I	<i>C. ellipsoideum</i> var. <i>minor</i> Bacilb.	W. & G. S. West, 1905	16-42	11-29	4-8	Probably world-wide	Apex rounded; sinus more closed
8, F, G	<i>C. contractum</i> Kirchn.	W. & G. S. West, 1905	31-41	25-31	7-9	Probably world-wide	Sinuc, tending to be obconcate; zygosporc angular
8, D	<i>C. contractum</i> f. <i>jacobsenii</i> (Roy) W. & G. S. West	Jacobsen, 1876	28-45	18-27	4-8	Europe, Asia, Africa, N. America	Proportionally more elongate
8, E	<i>C. contractum</i> var. <i>gartanense</i> W. & G. S. West	W. & G. S. West, 1905	68	43-44	10	British Isles, Scandinavia	Large form; apex retuse in middle
8, H	<i>C. subversum</i> Borge	Borge, 1897	24-26	18-20	9	Scotland	Obconcate sinuc; ist. rather wide
8, J	<i>C. füllebornii</i> Schmidle ²	Schmidle, 1902	60-873	46-643	21	Central and South Africa, Brazil	Large; chloropl. parietal
8, L	<i>C. contractum</i> var. <i>papillatum</i> W. & G. S. West	W. & G. S. West, 1896	73	51	20	North America	Large; chloropl. not known. Papillae on lateral margins
8, K	<i>ditto</i> , f. <i>minor</i> G. M. Smith	G. M. Smith, 1922	31-38	27-30	8-10	North America	Papillae on lateral margins
8, M	<i>C. lobatum</i> Boergesen	Borge, 1925	57-64 76-874	38-43 45-614	13-16 21-234	Brazil	End-view not far from circular; papillae on lateral margins
8, N (end-view)	<i>C. lobatum</i> var. <i>triquetrum</i> Grönblad	Grönblad, 1944	64	47	—	Brazil	To <i>Cosmostauracrum</i>
8, O	<i>C. lobatum</i> var. <i>ellipticum</i> Fritsch & Rich	Fritsch & Rich, 1937	44-68	38-48	17-19	Transvaal, Brazil	End-view broadly elliptical
8, P	<i>C. indentatum</i> Grönblad	Grönblad, 1920	50	30	8	Central Europe, Russia, Finland	Apex flattened; face of semicell thickened
8, Q	<i>C. foveatum</i> Schmidle f. <i>major</i> Borge	Borge, 1913	43-46	32-35	9-11	Scandinavia ⁵	Face of semicell with a large fovea
8, S	<i>C. scabratum</i> W. & G. S. West	W. & G. S. West, 1896	42	35-39	16-19	Central and South Africa	Comparatively short; minutely granulate; end-view subrhomboid
8, T	<i>C. trachydermum</i> W. & G. S. West var. <i>ellipticum</i> W. & G. S. West	W. & G. S. West, 1907	53	38-40	19	Burma	Granulate

8, R	<i>C. glaphyrodendrum</i> W. & G. S. West	W. & G. S. West, 1907	57-62	42-45	11-5	Burma	Granulate
8, V	<i>C. paracolum</i> Turner	Huber-Pestalozzi, 1936	80	60	34	India, Java; <i>forma</i> in East Africa	Granulate
8, U	<i>C. denotaris</i> (Witt.) Nordst.	De Notaris, 1867 ⁵	90-119	68-75	27	Scandinavia, Italy, Scotland	Large, with scrobulate wall; chloroplast imperfectly known
8, W	<i>C. dentatum</i> Wille	W. & G. S. West, 1896	110-111? 135-169	69-70? 88-96	23-24? 31-33	Canada, U.S.A., Cuba	Large; semic. somewhat trapezoid with thickened faces
9, A	<i>Staur. ellipticum</i> W. West	Sampaio, 1944	42-46	29-30	13-15	Britain, Portugal, Paraguay, Brazil	Isthmus rather broad
9, B	<i>S. muticum</i> Bréb. var. <i>viduariae</i> G. S. West	G. S. West, 1909	30	20-5	7-5	Australia	Probably a distinct species
9, D	<i>S. rotundatum</i> Turner	Turner, 1892	38	30	8	India, Canada	Cf. <i>Cosm. ellipsoidum</i> f. <i>retusa</i> (fig. 8, C)
9, E	<i>S. turgescens</i> De Not.	W. & G. S. West, 1902	28-39	25-33	10-12 18-20	Widely distributed in N. Hemisphere; a form recorded from Tanganyika	Minutely granulate
9, C	<i>S. subgrande</i> Borge	Borge, 1913	76-83	57-59	18-20	America, Kurile Isles	Cf. <i>Cosm. contractum</i> (fig. 8, F)
9, F	<i>S. subcornutum</i> De Toni	Borge, 1918	71-77	53-57	15-20	South America	Angles spinous
9, G	<i>S. brachyacanthum</i> Borge	Borge, 1918	20-22	18-19	8	Brazil	Comparatively short
9, H	<i>S. ocelluoides</i> Turner	Turner, 1892	20-23	18-20	7	India	Description inadequate
9, I	<i>S. tumidum</i> Bréb.	Prescott, 1935	121-134	90-127	44-50	Northern Hemisphere, a var. recorded from Brazil	Very large; membrane scrobiculate; chloroplasts parietal
9, L	<i>S. polytrichum</i> (Perty) Rabenh.	W. West, 1891	48-67	41-48	15-22	Europe, Asia, America	Semicells with regularly arranged spines
9, K	<i>S. cumbriae</i> W. West	W. West, 1891	76-85	55-65	25	Britain, Scandinavia	Semicells obtusate (cf. figs. 8, F; 9, C)
9, J	<i>S. saxonicum</i> Bulnh.	Roy & Bisset, 1894	77-79	58-65	21-22	Europe, North America; forms recorded from South America	Semicells more rounded, covered with short spines
9, M	<i>S. sagittiferum</i> Boerges.	Boergesen, 1890	41 (sine sp.)	35 (sine sp.)	13	Brazil, Paraguay	End-view with specialized outline
9, N	<i>S. ardiscon</i> (Ehrenb.) Lund.	Telling, 1944	66-66 (sine proc.)	46-48 (sine proc.)	24-33	Northern Hemisphere, var. recorded from Brazil	Semicells with two series of long arms; chloroplasts axile
9, O	<i>S. cetrulus</i> Grönblad	Grönblad, 1944	34 (sine proc.)	23 (sine proc.)	13	Brazil	Semicells with three bifid arms

¹ In most instances decimals have been ignored.

² Cf. *C. contractum* Kirchn. var. *maximum* W. & G. S. West (1896, p. 252).

³ Cf. Grönblad, 1944, p. 18.

⁴ Measurements given by Grönblad, 1944, p. 19.

⁵ *Cosmerium incavatum* Playfair (1807, p. 169) from New South Wales is similar to the present *C. glaphyrodendrum*, but the form of *C. rotundatum* of C. J. Schindler.

⁶ As *C. tetraphyllum* (De Notaris, 1867, p. 38, t. 3, f. 19).

⁷ Measurements given by Borge, 1909, p. 7.

owing to the unmodified elliptical shape of the semicells in front-view, the smooth globular zygosporangium (fig. 8, B), and the world-wide distribution, should probably be maintained as a distinct species. It has been found with zygosporangia in many parts of the world. The range of shape exhibited by the forms and varieties referred to *C. ellipsoideum* (figs. 8, A, C, I) is not considerable, but sufficient to indicate various potentialities. *C. contractum* Kirchn. (fig. 8 F) itself, including the f. *jacobsonii* (fig. 8, D), shows a distinct tendency towards an obcuneate shape of semicell and has a zygosporangium (fig. 8, G) with a more specialized outline than that of *C. ellipsoideum*. A closely related, though less deeply constricted, form is *C. subaversum* Borge (fig. 8, H). Special developments are seen in *C. indentatum* Grönblad (fig. 8, P), so far only found in parts of Europe, where the face of the semicell is thickened, and in *C. foveatum* Schmidle (fig. 8, Q), recorded from Scandinavia, where there is a large fovea on the face of each semicell.

The larger *C. contractum* var. *gartanense* W. & G. S. West (fig. 8, E), at present recorded only from the British Isles and Scandinavia, has subcircular semicells with a depressed apex. Other forms of large dimensions referred to *C. contractum*, have been described from the United States, namely var. *maximum* W. & G. S. West (1896; $84-89 \times 61-62 \mu$) and var. *papillatum* W. & G. S. West (fig. 8, L, also recorded from Canada); in the case of the former the authors state that there were no intermediates between it and the type. Comparable forms are known from the Southern Hemisphere, namely *C. füllebornei* Schmidle (fig. 8, J) from Africa and Brazil, *C. lobatum* Boergesen (fig. 8, M) from Brazil, and the smaller *C. lobatum* var. *ellipticum* Fritsch & Rich (fig. 8, O) from the Transvaal and Brazil. It is of interest to note that a much smaller form of *C. contractum* var. *papillatum* (fig. 8, K) has been found in the United States and that Grönblad (1944) has described a var. *triquetrum* (fig. 8, N) of *C. lobatum* from Brazil. These diverse forms are probably more closely related than their present reference to a number of species suggests. The chloroplasts are known only in *C. lobatum* (axile, fig. 8, M) and *C. füllebornei* (parietal, fig. 8, J).

All the forms, so far referred to, are non-ornamented, apart from the papillae of *C. contractum* var. *papillatum* and *C. lobatum*, but other species that appear to belong to this group have a membrane which is ornamented in various ways. Of these, only the rare *C. denotarisii* (Witttr.) Nordst. (fig. 8, U), a comparatively large species with densely and concentrically arranged scrobiculi, is known from Europe. Among the granulate species are: *C. paradoxum* Turner (fig. 8, V) found in Southern Asia (though a form has been recorded from East Africa); *C. trachydermum* W. & G. S. West var. *ellipticum* W. & G. S. West (fig. 8, T) from Burma; *C. scabraticum* W. & G. S. West (fig. 8, S) from Central and South Africa; and the more complex *C. glaphyronotum* W. & G. S. West (fig. 8, R) from Burma. Of these only the first reaches any considerable size. A more distinctive type is the North American *C. dentatum* Wolle (fig. 8, W) which in part attains very considerable dimensions and shows a distinctive ornamentation; the somewhat specialized shape and the thickened scrobiculate area on the face of the semicells mark a more fundamental departure from the basic type.

The staurostroid equivalent of *C. ellipsoideum* is *Staurostrum ellipticum* W. West (fig. 9, A), a rare species which will probably be found to have a wide distribution. The front-view of *S. rotundatum* Turner (fig. 9, D) is almost an exact replica of *C. ellipsoideum* f. *retusa* (fig. 8, C); originally described from India, it has recently been found in Canada (Irénee Marie, 1951) and will probably likewise prove to have a wide distribution. Parallel with *C. contractum* we have *S. subgrande* Borge (fig. 9, C), which is, however, about twice as big as the former and so far only known from America and the Kurile Islands. The giant *S. tumidum* Bréb. (fig. 9, I) is widespread over the Northern

Hemisphere and a variety is recorded from Brazil. Among the granulate species are : *S. turgescens* De Not. (fig. 9, E), widespread but seemingly confined to the Northern Hemisphere, although a form has been recorded from Lake Tanganyika ; the Australian *S. muticum* Bréb. var. *victoriense* W. & G. S. West (fig. 9, B) which should probably be a distinct species ; the rather doubtful *S. ochthodes* Turn. (fig. 9, H) from India ; and *S. brachyacanthum* Borge (fig. 9, G) from Brazil. The rather large and distinctive *S. subcornutum* De Toni (fig. 9, F) has been recorded several times, but only from South America.

Several more elaborately ornamented species of *Staurastrum* belong to this group, namely *S. saxonicum* Bulnh. (fig. 9, J) and *S. polytrichum* (Perty) Rabh. (fig. 9, L), both widespread in the Northern Hemisphere, the second also reported from South America. *S. cumbricum* W. West (fig. 9, K), in which the semicells again show the obcuneate shape, is known only from North Europe. These three species are all of some size, but the striking *S. sagittiferum* Boergesen (fig. 9, M), recorded only from South America, has dimensions more like those of a *C. ellipsoideum*. *S. arctiscon* (Ehrenb.) Lund. (fig. 9, N) and *S. circulus* Grönblad (fig. 9, O) differ from all the others, which should be regarded as species of *Cosmostaurastrum*, in the fact that the cell-body is produced into long arms, numerous in the former, only three in number in the latter ; *S. arctiscon* is recorded from many parts of the Northern Hemisphere, with varieties in Brazil, from which Grönblad's species was described. Both species are only tentatively included in this group.

It seems that all the smooth unornamented species of this group (except *C. subaversum*) have a wide distribution over the surface of the earth, but that the more specialized forms occupy more limited areas. It is noticeable that only one of these is so far recorded from Australia. The chief centres of development appear to be Tropical Asia and Tropical South America, although Tropical Africa may prove to be just as rich. The large species (*C. denotarisii*, *C. dentatum*, *St. tumidum*) have not so far been found outside the Northern Hemisphere, to which the more widely distributed staurastroid types are confined.

The two examples just considered will serve to show the kind of information that can be gleaned by this method of treatment, but it will not be until all the many species-groups have been assembled that it will be possible to tell a more complete story of parallel development and geographical distribution.

LITERATURE.

- BOERGESEN, F. 1890. *Vidensk. Medd. dansk. Naturh. Foren. Kbh.*, 929.
 —. 1901. *Botany of the Faeroes*, Copenhagen, 1, 198.
 BOHLIN, K. 1901. *Bih. svensk. Vetensk.-Akad. Handl.*, 27, III, No. 4.
 BERGE, O. 1897. *Bot. Notiser*, 211.
 —. 1899. *Bih. svensk. Vetensk.-Akad. Handl.*, 24, III, No. 12.
 —. 1903. *Ark. Bot.*, 1, 71.
 —. 1909. *Ibid.*, 8, No. 13.
 —. 1913. *Bot. Notiser*, 1.
 —. 1918. *Ark. Bot.*, 15, No. 13.
 —. 1921. Die Algenflora des Tåkernes, in *Sjön Tåkernes Fauna et Flora*.
K. Svensk. Vetensk.-Acad. Stockholm.
 —. 1923. *Ark. Bot.*, 18, No. 10.
 —. 1925. *Ibid.*, 19, No. 17.
 BOURELLY, P. & MANGUIN, E. 1946. *C.R. Acad. Sci. Paris*, 222, 682.
 CARTER, N. 1920. *Ann. Bot.*, 34, 265.
 CEDERGREN, G. R. 1932. *Ark. Bot.*, 25 A, No. 4.
 DICK, J. 1919. *Kryptog. Forsch. Bayer. Bot. Ges. München*, 230.
 DE NOTARIS, G. 1867. *Elementi per lo studio delle Desmidiacee Italiane*. Genova.
 ELFVING, F. 1881. *Act. Soc. Fauna Flora fenn.*, 2, No. 2.
 FRITSCH, F. E. 1906. *Kew Bull.*, Addit. Ser., 5, 187.
 —. 1933. *Trans. S.E. Union Sci. Soc.*, 18.
 FRITSCH, F. E. & RICH, F. 1937. *Trans. roy. Soc. S. Afr.*, 25, 153.
 GRÖNBLAD, R. 1920. *Act. Soc. Fauna Flora fenn.*, 47, No. 4.
 —. 1944. *Act. Soc. Sci. fenn.*, N.S., B, 2, No. 6.

- HEIMERL, A. 1891. *Verh. Zool.-Bot. Ges. Wien*, **41**, 587.
 HUBER-PESTALOZZI, G. 1936. *Ber. schweiz. bot. Ges.*, **46**, 131.
 IRÉNÉE-MARIE, FRÈRE. 1951. *Nat. canad.*, **78**, 301.
 JACOBSEN, J. P. 1876. *Aperçu systématique et critique sur les Desmidiacées du Danemark*. Copenhagen.
 JAO, C. C. 1949. *Bot. Bull. Acad. Sinica*, **3**, 37.
 KRIEGER, W. 1936. *Hedwigia*, **76**, 95.
 LAGERHEIM, G. 1885. *Öfvers. svensk. Vetensk.-Akad. Förhandl.*, No. 7, 225.
 LUNDELL, F. M. 1871. *Nova Acta Soc. Sci. upsal.*, III, **8**.
 LÜTKEMÜLLER, J. 1893. *Öst. bot. Z.*, **43**, 5.
 MESSIKOMMER, E. 1927. *Biologische Studien im Torfmoor von Robenhausen*, etc. Diss., Zurich.
 MEYEN, F. J. F. 1828. *Nova. Acta Leop. Carol.* **14**, 768.
 NORDSTEDT, O. 1869. *Vidensk. Medd. dansk. Naturh. Foren. Kbn.*, No. **14**.
 —. 1875. *Öfvers. svensk. Vetensk.-Akad. Förhandl.*, No. **6**, 13.
 —. 1877. *Ibid.*, No. **3**, 15.
 NYGAARD, G. 1932. *Trans. roy. Soc. S. Afr.*, **20**, 101.
 PLAYFAIR, G. I. 1907. *Proc. Linn. Soc. N.S.W.*, **32**, 160.
 PRESCOTT, G. W. (& MAGNOTTA, A.). 1935. *Pap. Mich. Acad. Sci.*, **20**, 157.
 PRESCOTT, G. W. 1938. *Ibid.*, **23**, 203.
 PRINTZ, H. 1915. *K. norske Vidensk. Selsk. Skr.*, No. **2**.
 RALFS, J. 1848. *The British Desmidiaceae*. London.
 RICH, F. 1935. *Trans. roy. Soc. S. Afr.*, **23**, 107.
 ROY, J. & BISSET, J. P. 1894. *Ann. Scot. nat. Hist.*, **40**.
 SAMPAIO, J. 1944. *Desmídias Portuguesas*. Coimbra (*Publ. Inst. Bot. Dr. Gonçalo Sampaio, Fac. Cienc. Univ. Porto*, No. **15**).
 SCHMIDLE, W. 1901. *Hedwigia*, **40**, 45.
 —. 1902. *Bot. Jb.*, **32**, 56.
 SKUJA, H. 1937. *Algae*, in *Symbolae Sinicae. Bot. Ergäbn. Exped. Akad. Wiss. Wien n. Südwest-China 1914-18*, **1**, Vienna.
 —. 1949. *Nova. Acta Soc. Sci. upsal.*, IV, **14**, No. 5.
 SMITH, G. M. 1922. *Trans. Wis. Acad. Sci. Arts Lett.*, **20**, 323.
 STRØM, K. M. 1924. *Rev. algol.*, **1**, 127.
 —. 1926. *Skr. norske Vidensk. Akad.*, Oslo, **1**, No. 6.
 TAYLOR, W. R. 1934. *Pap. Mich. Acad. Sci.*, **19**, 217.
 TEILING, E. 1944. *Medlemsbl. f. Biol. Fören. Stockholm*.
 —. 1950. *Bot. Notisev*, 299.
 TURNER, W. B. 1892. *K. svensk. Vetensk.-Akad. Handl.*, **25**, No. 5.
 WEST, W. 1890. *J. R. micr. Soc.*, 277.
 —. 1892. *J. Linn. Soc. (Bot.)*, **29**, 103.
 WEST, G. S. 1899. *Ibid.*, **34**, 366.
 —. 1907. *Ibid.*, **38**, 81.
 —. 1909. *Ibid.*, **39**, 1.
 —. 1912. *Journ. Bot.*, **50**, 79.
 —. 1914. *Mem. Soc. Neuchâtel Sci. nat.*, 1013.
 WEST, W. & WEST, G. S. 1895. *Trans. Linn. Soc. (Bot.)*, **5**, 41.
 —. 1896. *Ibid.*, **5**, 229.
 —. 1897. *J. Linn. Soc. (Bot.)*, **33**, 279.
 —. 1902. *Trans. R. Irish Acad.*, **32** (B), 1.
 —. 1905. *A Monograph of the British Desmidiaceae*, **2**. Ray Society.
 —. 1906. *Trans. R. Irish Acad.*, **33** (B), 77.
 —. 1907. *Ann. R. bot. Gdn., Calcutta*, **6**, 175.
 —. 1908. *A Monograph of the British Desmídiaceae*, **3**. Ray Society.

OBITUARIES

Christopher Albert Walter Sandeman, who died on 20 April 1951, will be remembered in the history of South American botany as a distinguished explorer and collector in Peru. He was born on 25 November 1882, and was educated at Eton and Christ Church. A great part of his life before and between the World Wars was spent on the Continent, at first in Munich, and later in southern Spain and on the French Riviera, where he became a keen gardener. This pleasant existence was interrupted during the 1914-18 War when he served with Military Intelligence. Throughout this period he had shown no signs of wandering in wild places after plants, but the idea was germinating, and his imagination had been fired by the adventures in Amazonian Peru of an intimate

friend, whose remarkable letters to him he eventually published in the book, *No Music in Particular* (1943), which was a curiosity of the by-ways of war-time literature. In the late 'thirties Sandeman went to the Swiss Alps, where he found that he could stand the high altitudes and made his first collection of wild flowers. This was a trial trip and decided his future course: though already well on in middle life, he would explore for plants on the mountains and in the tropical forests of Peru and other Spanish-American countries, whose language he spoke so well.

In the spring of 1938 he landed at Callao, the port of Lima, crossed the Andes and descended the Rio Huallaga by raft, returning to the coast at Trujillo by Moyobamba and the Trans-Andean trade route. The diary of this expedition provided the material for that enjoyable book, *A Forgotten River*, which was published in 1939, just after the outbreak of the war. On his next trip Sandeman ranged widely in various Republics, from Colombia to Chile. After some months in England he was off once more, for his longest visit of more than two years. In June, 1942, he left Rio de Janeiro for São Paulo and crossed the state of Matto Grosso to the Bolivian border, descending the Rio Madeira to the Amazon and going upstream into Peru. During these two years he visited many parts of Peru, collecting very extensively, and returned to London late in 1944. In July of the following year he reached Peru for the last time, having journeyed from Buenos Aires and through Bolivia. His final South American expeditions were to various parts of Colombia, particularly around Bogotá, in Antioquia, and near Bucaramanga. As late as 1951, when he was well over sixty-five, he had hoped to join his friend, the American botanist, Dr. Richard Schultes, in his explorations of the Apoporis and Caquetá Rivers, but this was not to be.

Sandeman collected in all about 6,200 numbers of dried specimens and he presented the first set, together with many seeds for the Gardens, to the Kew Herbarium. A second, much less complete, set was given to the Oxford University Herbarium, and two or three hundred further duplicates have been available for North American institutions, while a set of his Colombian plants has been kept in Bogotá, in the Colombian National Herbarium. He was very methodical, both as organizer and collector, and dried his specimens beautifully, writing careful field-notes. He never hurried and, except when he was descending the rivers, would stay for a long time in a single locality, changing his papers on intermediate days. By these somewhat tortoise-like methods he achieved more for science than some professional botanists who visit South America and collect very large numbers of specimens of indifferent quality or without adequate notes. As he often stayed in little-known regions he discovered some outstanding new species. Many of these have already been described and bear his name, the most distinguished being a new genus of Melastomatacea *Sandemaniana lilacina* Gleason, which he found near Moyobamba. But no doubt there are dozens of other plants among his large collections which await description by monographers who will visit Kew or borrow the material.

Not content with his natural gift for writing, Sandeman became an experienced photographer, and no-one who is interested in Peru should miss his *Wanderer in Inca Land* (1948), which is a collection of magnificent camera studies accompanied by descriptive text. His reading of South American history and travel literature was wide, and this led him to an ever-increasing admiration for the great English explorer-botanist, Richard Spruce. He felt that the memory of this extraordinary man, whose energy and minute powers of observation, in spite of ill-health and countless obstacles, had thrown so much light on the vegetation of these tropical rivers, from the mightiest tree to the smallest epiphyllous liverwort, had never received the honour it deserved. He therefore wrote an excellent summary of Spruce's life and work

on the occasion of the centenary of his arrival in Pará in 1849 (see *Journ. Royal Hortic. Soc.* lxxiv, part 12, 531-544), gave a broadcast on Spruce in one of a series of Sunday evening talks, and dedicated to his memory an exquisitely written essay, *Thyme and Brgamot* (Dropmore Press, 1947), in which he paid a moving tribute to his hero and claimed, after long experience of both, that botanical exploration rather than gardening should receive the palm as 'the purest of human pleasures.'

It is evident that Sandeman enjoyed a full life, and used his ample leisure and resources to good purpose. He was a man of parts, and when he came back from the forests and mountains he could appear a very different person. A citizen of the world, in the finest sense of the term, he was a familiar figure in the social, diplomatic and theatrical circles of London. He was a playwright, a wit and a *raconteur*, with a remarkable memory for poetry, as well as an excellent linguist and a shrewd observer of the international scene and of the 'new order' at home. Behind everything, of course, was his love of beauty and quality; and behind the urbanity and *savoir-vivre* was the lively, interesting, lovable friend who put you completely at your ease and who, as someone has said elsewhere, was "equally at home with the great ones of the world or the simple Indians of the Peruvian mountains".

Like Spruce, he did not marry. He was admitted a Fellow of the Linnean Society on 12 May 1949, and was a generous donor to its library.

N. Y. SANDWITH.

Anthony Belt, F.L.S. (1862-1952). Although it is customary in the Society's *Proceedings* to give an impersonal account of the life of a deceased Fellow, Mr. Belt had already left a modest and adequate memoir of his own, prepared in the first instance for the use of the local press. His autobiographical statement is therefore printed below. It only remains to add, what Mr. Belt could not accurately foresee, that his death took place on 19 April 1952. He was elected a Fellow of the Linnean Society in 1910. W.E.S.

ANTHONY BELT, F.L.S.

My father, Thomas Belt, F.G.S., of Newcastle-on-Tyne, was from his early days very much drawn to the study of natural history, and his book "The Naturalist in Nicaragua" is a classic. He was by profession a mining engineer, and I was born at Halifax, Nova Scotia (12 September 1862) when he was in charge of gold mines in that province. From him I inherited the love of natural history, fostered by 18 months spent with him amid the tropical luxuriance of Nicaragua, which has been the cause of much of the happiness in my life.

Always of a delicate constitution, I was not strong enough for boarding-school life and was privately educated at home. The sudden death of my father in 1878 put an end to plans for my going to Cambridge, and when the time came to take up a career I opened a preparatory school at Ealing which proved very successful. Joining the local Natural History and Microscopical Society, I was its hon. secretary for 11 years when reasons of health resulted in my going to live with my mother at St. Leonards on Sea in 1899. I took private pupils here until 1914, and married in 1925 the daughter of the late Cyril Davenport, F.S.A., of the British Museum. I joined the Hastings and St. Leonards Natural History Society, was its treasurer and editor for many years, and in 1927 succeeded the late Thomas Parkin, F.L.S., F.Z.S., F.R.G.S., as president, a position I still hold.

I have done little scientific research beyond compiling local faunal lists, but for over 60 years have had a part in the development and maintenance of an interest in natural science through my connection with scientific

movements in Ealing and Hastings. I have also been particularly interested in the Hastings Museum and public Library, and have been vice-chairman of the municipal Museum and Library Committee for some 35 years.

In other intellectual movements in Hastings I was for many years president or chairman of the Egyptian Society and the local branch of the University Extension Association, and for a shorter period (until during the Great War it ceased to be a council governed school) of the Hastings and St. Leonards Ladies' College. For over 25 years I was a Manager of the Municipal Schools of Science and Art and a member of the Literary Society. I am also an original member of the Twenty Club, a dining club for those interested in literature science and art, and for the entertaining of distinguished visitors to the town. Outside the town my chief scientific work has been connected with the South-eastern Union of Scientific Societies of which I am a vice-president.

Owing to my distance from London I have seldom been able to attend the meetings of the Linnean Society though I did take part in the memorable celebration of its 150th Anniversary, and have more than once sent specimens of plant abnormalities for exhibition at the meetings.

I shall not be remembered for any outstanding achievement, but hope that in a quiet way I have really been able to help forward the local scientific and educational movements with which I have been so long associated.

ANTHONY BELT.

11 June 1944.

The untimely death of Dr. **Walter Robert Ivimey Cook**, F.L.S. on 1 February 1952 at the age of 50 was a sad loss to Botany and to Mycology in particular.

Dr. Cook was born in London in 1901 and was educated at Dulwich College, where he first acquired his interest in Biology. He studied Botany at King's College, London, where he took his degree in 1923. After graduating, he stayed on at King's College as Junior Demonstrator in Botany, becoming specially interested in Mycology. This interest was to a great extent prompted by the work of that quaint, and now almost forgotten, character on the botanical staff at King's, Dr. E. J. Schwartz. It was in these years that Cook began an intensive study of that out of the way group of organisms, the Myxomycetes, and especially of the Plasmodiophorales. In a succession of papers published over a number of years, he became the undoubted authority on that group in this country. In addition he made important contributions to our knowledge of other groups of the Fungi.

In 1928, he was appointed to the staff of the Botanical Department of the University of Bristol, and three years later moved to University College, Cardiff, where he remained for the rest of his life.

Cook's interests were not merely confined to the mycological side of Botany, and both at Bristol and at Cardiff he took a full part in all kinds of botanical teaching. An enthusiastic field worker, he was never happier than with a group of students on a foray. Cook's keenness for teaching early led him to embark on the writing of a series of text-books. The first was begun in collaboration with the present writer, while Cook was still only a junior demonstrator at King's. This was *Biology for Medical Students*, which in the course of a number of editions published since 1931 has become very familiar to countless medical and other first year students of Biology. Not content with this, he had in more recent years produced, in collaboration with Professor R. C. McLean, books on Practical Plant Ecology and Botanical Formulae, and finally a comprehensive advanced Text-book of Botany in four volumes. It is a tragedy that Cook did not live to see the completion of this mighty work to which he had contributed so much.

Robin Cook was an enthusiast. He had three great loves, Botany, his garden and his home. To these three he devoted his life, almost to the exclusion of everything else. Unlike some academic botanists, he was a real practical gardener, as his garden attached to his home at Dinas Powis, near Cardiff, is ample evidence. Not only did he know what plants to grow and how to grow them (and fruit and vegetables for the kitchen were there, as well as flowers and strange plants intriguing to the botanist), but he was to a great extent his own contractor, building with his own hands walls, fences, green-houses and sheds, all with expert skill. He spent most of his spare time on work of this kind and he was at his happiest in his workshop. During the Second World War, he turned part of his garden into a miniature farm and kept cows, pigs and goats in addition to the more orthodox animals of a garden such as chickens and rabbits. And there must always be dogs to play around him as he worked and a pipe to be smoked. How he found time for all his manifold activities both at the University and at home is a mystery (during the War he also acted as a Special Constable in the village), but no doubt it was because he was so full of abounding energy. These were the things he liked and therefore he devoted his whole time, his whole heart and his whole soul to them. He rarely left his home other than for something connected with his work. He was not keen on travelling, because he obtained so much satisfaction in his work at College and at home.

As one who collaborated with him and had known him since both were students together, the present writer can think of him only with affection and a deep sense of loss. In collaboration, Robin Cook took his full share of the work, and had strong views, which he expressed in that loud, vigorous voice of his, not only on his own part of the work, but also he had sound and valuable criticisms of that done by his collaborator. In turn, he would listen seriously to criticisms of his own work, and, though this often led to spirited argument, there were no hard feelings and in the end the difficulties and differences were always completely ironed out to the satisfaction of all. Collaboration with Cook meant much stimulating discussion and laughter, but no anger or tears.

Robin Cook married twice, first to Awdrey Hooton, who died in 1935, leaving him with two young sons, and secondly to Muriel Taylor, who cared so tenderly for the home he loved so much. Our deepest sympathy goes out to Mrs. Cook and the two boys.

C. C. HENTSCHEL.

Arnold Swaffer (1926–1951). The death under tragic circumstances of Arnold Swaffer in the spring of 1951 deprives our Society of a young botanist of considerable promise. Born on 16 March 1926, he was educated at Whitgift School and won an open Exhibition to Sidney Sussex College, Cambridge, subsequently becoming a Minor Scholar. After obtaining Honours in both parts of the Natural Sciences Tripos and graduating B.A. (1947), he was appointed Research Assistant in Cotton Physiology at Manchester University. While holding this post he investigated the morphogenesis of the cotton hair and the respiration of the cotton ovule. His interests in botany were wide, but his chief love was for cytology and in 1949 he was promoted to be Assistant Lecturer 'in Botany and Zoology with special reference to cytology'. During the summer of 1950 he spent some months in Professor Caspersson's laboratory at Stockholm to gain experience of nucleic acid studies. He was by no means exclusively a laboratory worker and was an accomplished field botanist. In association with Mr. Oleg Polunin he made a study of *Clematis vitalba* for the *Biological Flora* which it is hoped will soon be published.

Swaffer became an Ordinary Associate of the Linnean Society in 1947. He showed an attractive eagerness and enthusiasm in everything he undertook; he had a quick and keen intelligence. We mourn the loss of one cut off before his talents had come to fruition.

PAUL RICHARDS.

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Note.—Names of donors are given in square brackets. Separate copies of papers which are included in periodicals received by the Library are no longer catalogued.

- Blair, Alan.** *See Hagberg, Knut.*
- Bowles, E. A.** A Handbook of Crocus and Colchicum for gardeners. Pp. 222. 8vo. London, 1952. [AUTHOR.]
- Broom, Robert, & Robinson, J. T.** Swartkrans Ape-Man (*Paranthropus crassidens*). Pp. 124. 4to. *Parow*, 1952.
- Buckley, T. E., & Harvie-Brown, J. W.** A vertebrate fauna of the Orkney Islands. Pp. xxiv+314. 8vo. *Edinburgh*, 1891.
- Carnegie Institution of Washington.**
- CAMPBELL, A. S. The Oceanic Tintinnoida of the Plankton gathered during the last cruise of the "Carnegie". Pp. vi+164. (Publ. No. 537.) 4to. *Washington*, 1942.
- CLEMENTS, F. E., WEAVER, J. E., & HANSON, H. C. Plant competition; an analysis of community functions. Pp. xvi+340. (Publ. No. 398.) 8vo. *Washington*, 1929.
- GOLDER, FRANK A. Guide to materials for American History in Russian Archives. 2 vols. (Publ. No. 239, 1 and 2.) 8vo. *Washington*, 1917-37.
- GRAHAM, H. W. Studies in the morphology, taxonomy and ecology of the Peridiniales. Pp. viii+130. (Publ. No. 542.) 4to. *Washington*, 1942.
- JOHNSON, R. H. Determinate evolution in the color-pattern of the lady-beetles. Pp. vi+104. (Publ. No. 122.) 8vo. *Washington*, 1910.
- LLOYD, FRANCIS ERNEST. Guayule. (*Parthenium argentatum*, Gray.) A rubber plant of the Chihuahuan Desert. Pp. viii+214. (Publ. No. 139.) 8vo. *Washington*, 1911.
- McMURRICH, J. PLAYFAIR. Leonardo da Vinci. The Anatomist. (1452-1519.) Pp. xx+266. (Publ. No. 411.) 8vo. *Washington*, 1930.
- Papers from Tortugas Laboratory, Vol. XXXV. The photodynamic action of dyes on the eggs of the Sea Urchin, *Lytechinus variegatus*. Pp. 154. (Publ. No. 539.) 8vo. *Washington*, 1942.
- REICHERT, EDWARD TYSON. A Biochemic basis for the study of problems of taxonomy, heredity, evolution, etc., with special reference to the starches and tissues of parent-stocks and hybrid-stocks and the starches and hemoglobins of varieties, species and genera. 2 parts. (Publ. No. 270.) 8vo. *Washington*, 1919.
- STURTEVANT, A. H., & DOBZHANSKY, T. Contributions to the genetics of certain chromosome anomalies in *Drosophila melanogaster*. Pp. 82. (Publ. No. 421.) 8vo. *Washington*, 1931.
- WHITE, DAVID. Flora of the Hermit shale, Grand Canyon, Arizona. Pp. 222. (Publ. No. 405.) 8vo. *Washington*, 1929.
- WILLIS, BAILEY. East African Plateaus and Rift Valleys. Pp. x+358. (Publ. No. 470.) 4to. *Washington*, 1936.
- WILSON, C. B. The Copepods of the Plankton gathered during the last cruise of the "Carnegie". Pp. iv+238. (Publ. No. 536.) 4to. *Washington*, 1942.
- Clapham, A. R., Tutin, T. G., & Warburg, E. F. Flora of the British Isles. Pp. li+1592. 8vo. *Cambridge*, 1952. [CARNegie INST.]
- Deacock, R. J. *See Prime, C. T.* [AUTHORS.]
- Evans, A. H.** A fauna of the Tweed Area. Pp. xxviii+262. 8vo. *Edinburgh*, 1911.
- , & **Buckley, T. E.** A vertebrate Fauna of the Shetland Islands. Pp. xxx+248. 8vo. *Edinburgh*, 1899.
- Feldmann, Jean.** Recherches sur la végétation marine de la Méditerranée. La Côte des Albères. Pp. 340. (Rev. Algologique, 10, 1937.) 8vo. *Paris*, 1937. [AUTHOR.]
- , Les Algues marines de la Côte des Albères, I-IV. Cyanophycées, Chlorophycées, Phaeophycées, Rhodophycées. Pp. 372. 8vo. *Paris*, 1937-42. (Rev. Algol. 9, 1937.) [AUTHOR.]
- Fournier, P.** Les quatre flores de la France. Pp. xlviii+1091. 8vo. *Paris*, 1946.
- Graham, H. D.** The Birds of Iona and Mull. Pp. xvi+280. 8vo. *Edinburgh*, 1890.
- Hagberg, Knut.** Carl Linnaeus. Translated from the Swedish by ALAN BLAIR. Pp. 264. 8vo. *London*, 1952. [ANGLO-SWEDISH LITERARY FOUNDATION.]

- Harvie-Brown, J. A.** A Fauna of the Tay Basin & Strathmore. Pp. lxxxvi+378. 8vo. *Edinburgh*, 1906.
- , & **Buckley, T. E.** A vertebrate fauna of Sutherland, Caithness and West Cromarty. Pp. xii+344. 8vo. *Edinburgh*, 1887.
- , —. A vertebrate fauna of the Outer Hebrides. Pp. xciv+280. 8vo. *Edinburgh*, 1887.
- , —. A vertebrate fauna of Argyll and the Inner Hebrides. Pp. lxxxiv+262. 8vo. *Edinburgh*, 1892.
- , —. A fauna of the Moray Basin. 2 vols. 8vo. *Edinburgh*, 1895.
- , & **Macpherson, H. A.** A fauna of the North-West Highlands and Skye. Pp. civ+378. 8vo. *Edinburgh*, 1904.
- Journal of Experimental Botany.** Vol. 1, → 8vo. *Oxford*, 1950 →
- Matthews, L. Harrison.** British Mammals. Pp. xii+410. (New Naturalist Series.) 8vo. *London*, 1952.
- Prestwich, A. A.** Records of Parrots bred in captivity. Pt. V. Lovebirds & Broadtails. Pp. 108. 8vo. *London*, 1952. [AUTHOR.]
- Prime, C. T., & Deacock, R. J.** Trees and Shrubs: their identification in Summer or Winter. Pp. 110. 8vo. *Cambridge*, 1952. [C. T. PRIME.]
- Robinson, J. T.** See **Broom, Robert.**
- Rothschild, Miriam, & Clay, Theresa.** Fleas, Flukes and Cuckoos. Pp. xiv+304. (New Naturalist Series.) 8vo. *London*, 1952.
- Tutin, T. G.** See **Clapham, A. R.**
- Visher, S. S.** Indiana Scientists. Pp. viii+286. 8vo. *Indianapolis*, 1951.
- Warburg, E. F.** See **Clapham, A. R.**

INSCH TEA LIBRARY

- Aird, J. E.** A handbook of tables and memoranda for planters. Pp. 85. 8vo. *Calcutta*, 1905.
- Allen Bros. & Co.** Practical points for Tea Planters. Pp. 68. 8vo. *Calcutta* (s.a.).
- , —. Tea fertilization in India. Pp. 58. 8vo. *Calcutta* (s.a.).
- An Act of Parliament concerning duties upon tea, coffee, etc.** Pp. 18. fol. *London*, 1704.
- Anand Mulk Raj.** Two leaves and a bud. Pp. 258. 8vo. *London*, 1937.
- Andrews, E. A.** Factors affecting the control of the Tea Mosquito Bug. (*Helopeltis theivora* Waterh.) Pp. 260. 8vo. *London*, 1923.
- , & **Tunstall, A. C.** Notes on the spraying of tea. Pp. 76. 8vo. *Calcutta*, 1915.
- Antram, C. B.** The Bark-eating Borers of tea. Pp. 18. 8vo. *Calcutta*, 1907.
- , —. The "Thrips" Insects of Tea in Darjeeling. Pp. 10. 8vo. *Calcutta*, 1909.
- Ashplant, Herbert.** Report on Mosquito blight (*Helopeltis*) of tea in Java with description of combative measures used and with special reference to the alternate row pruning system. Pp. 41. 8vo. *Mundakayam*, 1924.
- Assam.** Sketch of its history, soil, and productions; with the discovery of the Tea-plant. Pp. 57. 8vo. *London*, 1839.
- , —. Nowgong Tea Company. Reports 1866. 8vo. *London*, 1866.
- Baildon, Samuel.** Tea in Assam. Pp. 66. 8vo. *Calcutta*, 1877.
- , —. The Tea Industry in India. Pp. 248. 8vo. *London*, 1882.
- Bald, Claud.** Experiments in manuring on a tea estate in Darjeeling. (Agric. Journ. India, 8.)
- , —. Green manuring on tea estates. (Agric. Journ. India, 9.)
- , —. Indian Tea: its culture and manufacture. Eds. 1, 3 and 5. 8vo. *Calcutta*, 1903-40.
- Ball, Samuel.** An account of the cultivation and manufacture of tea in China. Pp. xx+382. 8vo. *London*, 1848.
- Bamber, E. F.** An account of the cultivation and manufacture of tea in India, from personal observation. Pp. 92+x. 8vo. *Calcutta*, 1866.
- Bamber, M. Kelway.** A text-book on the chemistry and agriculture of tea including the growth and manufacture. Pp. 258+xxii. 8vo. *Calcutta*, 1893.
- , —. Ceylon tea soils and their effects on the quality of tea. Pp. 16. 8vo. *Kandy*, 1900.
- , & **Holmes, J. A.** Experimental tea plots, Peradeniya. (Circ. Roy. Bot. Gdns. Ceylon, 5, 1911.)
- Barker, George M.** A Tea Planter's Life in Assam. Pp. 248. 8vo. *Calcutta*, 1884.
- Basu, B. C.** The cultivation of pulse crops in the Assam Valley. (Agric. Ledger, 1903.)
- Bentley, C. A.** Report on the health of the labour force at Jiti Tea Estate, Dooars. Pp. 25. 8vo. *Calcutta*, 1909.
- Bergsma, Cornelius Adrian.** Dissertatio inauguralis Botanico-Medica de Thea. . . . (And translation.) Pp. xvi+52+48. 8vo. (s.l.), 1825.
- Bishop, P. O.** Sketches in Assam. Pp. ix+257. 8vo. *Calcutta*, 1885.
- Blancard, Stephan.** Haustus Polychresti, oder zurverlässige bedanken vom Theé, Coffée, Chocolate, und Taback. 8vo. *Hamburg*, 1705.
- Blount, Thomas Pope.** A natural history: containing many not common observations: extracted out of the best modern writers. Pp. xiv+472. 8vo. *London*, 1693.

- Borrich, Ola.** De usuplantarum, indigenarum in medicina, et sub finem, de Clysse plantarum, Thee specifico. 8vo. *Hafniae*, 1690.
- Boutilly, V.** Le Thé, sa culture et sa manipulation. (and translation.) Pp. 108. 8vo. *Paris*, 1898.
- Brace, E.** Tea cultivation in Southern India and Ceylon. Pp. 84. 8vo. *Colombo*, 1880.
- Breyn, J.** Plantarum exoticarum. Pp. xxxiv+104+xxv and pls. 101. 4to. *Danzig*, 1678.
- Britannicus.** The tea industry in Assam. Pp. 104+15. 8vo. [s.l.], 1886.
- Browne, Edith A.** Peeps at Industries: Tea. Ed. 2. Pp. viii+88. 8vo. *London*, 1917.
- Bruce, C. A.** Report on the manufacture of tea, and on the extent and produce of the Tea Plantations in Assam. (Jnl. Asiatic Soc. Bengal, 1839.)
- Buckingham, James.** A few facts about Indian tea. Pp. 31. 8vo. *London* (s.a.).
- Bulletin of the Research Institute of the Tea industry in the U.S.S.R.** No. 2. fol. *Tiflis*, 1931.
- Burkill, I. H.** Bat and Bird Guanos in India. (Agric. Ledger, 1911.)
- Carpenter, P. H.** Report on a visit to Java and Sumatra. Pp. 100. 8vo. *Calcutta* (s.a.).
- Report of two lectures on the Tea plant and Tea manufacture. 8vo. *London*, 1927.
- , & **Andrews, E. A.** A note on the value of different insect control methods in tea and against mosquito blight in particular. Pp. 24. (Indian Tea Association.) 8vo. *Calcutta*, 1922.
- , & **Harrison, C. J.** The manufacture of tea in North-East India. Pp. 42. (Indian Tea Association.) 8vo. *Calcutta*, 1927.
- Cave, H. W.** Golden Tips. A description of Ceylon and its great Tea Industry. Pp. xii+476. 8vo. *London*, 1901.
- (The) Ceylon Planter's "vade mecum".** Pp. 42. 8vo. *Colombo*, 1891.
- Chamney, Montfort.** The story of the tea leaf. Pp. 78. 8vo. *Calcutta* (s.a.).
- Chandler, S. E., & McEwan, John.** Tea: its cultivation, manufacture, and commerce. (Bull. Imperial Institute.) 8vo. *London*, 1913.
- Chaston, Chas. S.** Bamboo cultivation in Assam. Pp. 8. 8vo. (s.l.), 1924.
- China.** A glance at the interior of China obtained during a journey through the silk and green tea districts. Pp. 192. 8vo. (s.l.), 1845.
- Compton, Herbert.** Come to tea with us. Pp. 124. 8vo. *London*, 1905.
- Congreve, C. R. J.** The Anamallais. Pp. vi+152.
- Cotes, E. C.** An account of the insects and mites which attack the tea plant in India. Pp. 72+ii. 8vo. *Calcutta*, 1895.
- Cottam, H.** Tea Cultivation in Assam. Pp. 76. 8vo. *Colombo*, 1877.
- Coulombier, F.** L'Arbre à Thé. Pp. vi+164. 8vo. *Paris*, 1900.
- Cowie, G. A.** The fertilization of tea. Pp. 68. 8vo. *London* (s.a.).
- Cox, E. H. M.** Plant-hunting in China. Pp. 230. 8vo. *London*, 1945.
- Crawford, T. C.** Handbook of Castes and Tribes. Pp. 360. 8vo. *Calcutta*, 1924.
- Crole, David.** Tea; a text-book of tea planting and manufacture. Pp. xii+242. 8vo. *London*, 1897.
- Curtler, E. A.** The cultivation and manufacture of tea in Ceylon and India. Pp. 94. 8vo. *Kuala Lumpur*, 1932.
- D., A. F.** A tea trade with Thibet. Pp. 20. 8vo. *Calcutta*, 1833.
- The manufacture of tea. Pp. 20. 8vo. *Chittagong*, 1880.
- Daily Telegraph.** Supplement: The story of Empire tea. 28/2/38.
- Dangri & Dhonjan Tea Seed Co.** Tea seed. Pp. 22. 8vo. *Assam* (s.a.).
- Day, Samuel Phillips.** Tea: its mystery and history. Pp. xvi+17-92. 8vo. *London*, 1878.
- Deas, F. T. R.** The young tea-planter's companion. Pp. xii+96. 8vo. *London*, 1886.
- de Blegny.** Le bon usage du Thé, du Café et du Chocolat pour la preservation & pour la guérison des maladies. Pp. xx+362. 8vo. *Paris*, 1867.
- Denton, F. J.** Tea share manual. Pp. 254. 8vo. *London*, 1922.
- Dowling, A. F.** Tea notes. Pp. 117. 8vo. *Calcutta*, 1886.
- Dozey, E. C.** A concise history of the Darjeeling District since 1835 with a complete itinerary of tours in Sikkim and the District. Pp. xxvi+350. 8vo. *Darjeeling*, 1916.
- Dufour, Philippe Sylvestre.** Traitez nouveaux & curieux du Café du Thé et du Chocolate. Ed. 2. (and translation.) Pp. xx+54. 8vo. *Lyon*, 1688.
- Duncan.** Avis salutaire a tout le monde, contre l'abus des choses chaude, et particuliere-ment du Café, du chocolat, et du Thé. (and translation.) 8vo. *Rotterdam*, 1705.
- Dyke, W.** Manures and their application. Pp. 32. 8vo. *London*, 1895.
- East Indian Company.** September and December Sales. Black and Green Teas. 1836.
- Eden, Ashley.** Political Missions to Bootan, comprising the reports of 'The Hon'ble Ashley Eden—1864. 8vo. *Calcutta*, 1865.
- Elliott, E. C., & Whitehead, F. J.** Tea planting in Ceylon. Pp. xx+278. 8vo. *Colombo*, 1926.
- Encyclopaedia Britannica.** STR-TEU.
- Feistmantel, Ottokar.** Die Theekultur in British-ost-Indien. Pp. viii+100. 8vo. *Prag*, 1888.

- Fletcher, F.** Note on a toxic substance excreted by the roots of plants. (Mem. Dept. Agric. India, Bot. Ser., vol. 2, no. 3, 1908.)
- Foley, E. G.** Report on a visit to Meshed (Persia) via the Nushki-Seistan route. (Indian Tea Association.) Pp. 26. 8vo. *Calcutta*, 1901.
- Fortune, Robert.** Three years' wanderings in the Northern Provinces of China, including a visit to the tea, silk and cotton countries. . . . Pp. xiv+406. 8vo. *London*, 1847.
- Report upon the Tea Plantations in the North Western Provinces. Pp. 15. 8vo. *Calcutta*, 1851.
- Visit to the Tea Districts of China and India. Pp. xvi+398. 8vo. *London*, 1852.
- Two visits to the Tea Countries of China and the British Tea Plantations in the Himalayas. 2 vols. Ed. 3. Pp. xii+315 ; viii+298. 8vo. *London*, 1853.
- A residence among the Chinese : inland, on the coast, and at sea. Pp. xvi+440. 8vo. *London*, 1857.
- A narrative of a journey to the Capitals of Japan and China. Pp. xvi+395. 8vo. *London*, 1863.
- Fraser.** Rings from a Chota Sahib's pipe. Pp. 186. 8vo. *Calcutta*, 1901.
- Fraser, Wm.** The recollections of a Tea Planter. Pp. 226. 8vo. *London*, 1935.
- Fukukita, Yasunosuke.** Cha-No-Yu. Tea cult of Japan. Pp. xiv+112+xxxv. 8vo. *Tokyo*, 1932.
- Gait, Sir Edward.** A history of Assam. Pp. xx+388. 8vo. *Calcutta*, 1926.
- Gandhi, M. K.** The story of my experiments with truth. 2 vols. 8vo. *Ahmedabad*, 1927-29.
- Godfrey, Boyle.** Miscellanea vere utilia ; or miscellaneous experiments and observations on various subjects. Pp. 138. 8vo. *London*, [1735].
- Gordon, G. J.** Discovery of the genuine tea plant in Upper Assam. (Journ. Asiatic Society of Bengal, 1835.)
- Memorandum of an excursion to the Tea Hills which produce the description of tea known in commerce under the designation of Ankoy Tea. (Journ. Asiatic Society of Bengal, 1835.)
- Gow, Wilson Stanton.** Tea producing companies of India and Ceylon. Pp. x+172. 8vo. *London*, 1897.
- Greig, J. L.** The cultivation of lowland tea at the Central Experiment Station, Serdang. 8vo. *Kuala Lumpur*, 1937.
- Griffith, William.** Report on the tea plant of Upper Assam. Pp. 85. 8vo. *Calcutta*, 1838.
- Posthumous papers bequeathed to the Honorable the East India Company, and printed by order of the Government of Bengal. Journals of travels in Assam, Burma, Bootan, Afghanistan. 8vo. *Calcutta*, 1847.
- Gupta, Sasi Bhuson.** Tea-maker's pocket guide. Ed. 2. Pp. 22. 8vo. *Calcutta*, 1907.
- H. . . .** A Journal of eight days' journey from Portsmouth to Kingston upon Thames ; . . . with miscellaneous thoughts . . . to which is added an essay on Tea. 2 vols 4to. *London*, 1756-7.
- Hamlin, Edward.** Tea cultivation in Ceylon. Pruning and kindred subjects. Ed. 2. Pp. vi+28. 8vo. *Colombo*, 1905.
- Harington, J. E. M.** Tea in Europe. A study of the Continent as a Market for British-grown Tea. Pp. 64. 8vo. *Hitchin*, 1904.
- Haworth, W.** Notes and suggestions on the cultivation, manufacture and cost of production of tea in Cachar. Pp. iv+46. 8vo. *Calcutta*, 1867.
- Hillcoat, Chas. H.** Notes on stowage ; being a concise and handy *vade mecum* on all matters connected with the proper stowing of all kinds of cargo, with actual measurements. Pp. 180. 8vo. *London*, 1894.
- Hooper, David.** A report on the manufacture and composition of Indian saltpetre. (Agric. Ledger, 1905.)
- Hope, G. D.** Note on the cultivation of tea soils. (Indian Tea Association.) Pp. 7. 8vo. *Calcutta*, 1910.
- Lecture delivered at the Darjeeling Planter's Club. (Indian Tea Association.) Pp. 12. 8vo. *Calcutta*, 1911.
- Note on soil denudation by rainfall and drainage : conservation of soil moisture. (Agric. Journ. India, XI, pt. 2, 1916.)
- Report on certain aspects of the tea industry of Java and Sumatra. Pp. 122. (Indian Tea Association.) 8vo. *Calcutta*, 1916.
- Papers on soil denudation. (Indian Tea Association.) 8vo. *Calcutta*, 1917.
- Memorandum on the use of artificial manures on the Tea Estates of Assam & Bengal—Decade 1907-1917. With reprint of a memorandum on the use of artificial manures on the Tea Estates of Assam & Bengal prior to 1907. Pp. 42. 8vo. *Calcutta*, 1918.
- & **Antram, C. B.** Damage by beetles in tea chest woods. Pp. 13. 8vo. *Calcutta*, 1912.
- & **Carpenter, P. H.** Some aspects of modern tea pruning. Pp. 58. 8vo. *Calcutta*, 1914.

- Hopə, G. D., & Carpenter, P. H.** Suggestions for the manurial treatment of tea soils. (Indian Tea Association.) Pp. 88. 8vo. *Calcutta*, 1915.
- , —. Report on disease in Tea seed nurseries in Debrugarh and Doom Dooma Districts, Assam, during season 1909. 8vo. *Calcutta*, 1909.
- Horsfield, Thomas.** Essay on the cultivation and manufacture of tea in Java; taken from a periodical published at Batavia, under the title of "Tydschrift voor Neerlands Indie" Third year, No. 1. Translated from the Dutch. 8vo. *London*, 1841.
- Houssaye, J. G.** Monographie du Thé. (and translation.) Pp. 160. 8vo. *Paris*, 1843.
- Howard, Sir Albert.** Report on a tour to some tea estates in India and Ceylon. Pp. 32. 8vo. *London*, 1938.
- Hunter, W. W.** A Statistical Account of Assam. Vols. 1 and 2. 8vo. *London*, 1879.
- Hutchinson, C. M.** Report on investigations made as to the causes of taints in packed teas, 1908. (Indian Tea Association.) Pp. 14. 8vo. *Calcutta*, 1909.
- Hutchison, James.** Report on the cultivation and manufacture of Formosa Oolong Tea. Pp. 30. 8vo. *Calcutta*, 1904.
- , —. Indian Brick Tea for Tibet. Report on a mission to Ssu-chuan. Pp. 61. 8vo. *Calcutta*, 1906.
- Ibbetson, A.** Tea from grower to consumer. Pp. viii+116. 8vo. *London* (s.a.).
- India Tea, A few facts about.** (A Souvenir from the British Empire Exhibition.) 1924.
- Indian Tea Association.** Scientific Department Quarterly Journal. 1911-23, 1926-32.
- , —. Tocklai Experimental Station. Annual Report, 1936. 8vo. *Calcutta*, 1937.
- , —. Tocklai Experimental Station Memoranda, Nos. 1-4, 6. 8vo. *Calcutta*, 1938-9.
- , —. Tocklai Experimental Station. Proceedings at the First Annual Conference, held at Tocklai on the 18th, 19th and 20th February, 1937.
- , —. Tocklai Experimental Station. Proceedings of the Second Annual Conference, held at Tocklai on the 17th, 18th and 19th February, 1938.
- , —. Handbook of Information, 1917. Pp. 34. 8vo. *Calcutta*, 1917.
- , —. Scientific Department. Index to the issues of 1911-1932 of the Quarterly. Pp. 123. 8vo. *Calcutta*, 1935.
- , —. Scientific Department. Handbook of Information, 1929. Pp. 102. 8vo. *Calcutta*, 1929.
- , —. Report by Dr. H. H. Mann on his visit to Tocklai in April, 1927. 8vo. *Calcutta*, 1927.
- , —. Bacteria and the manufacture of Black Tea. By P. H. Carpenter & S. F. Benton. 8vo. *Calcutta*, 1933.
- , —. The use of E.C. in factories in theory and practice. 8vo. *Calcutta*, 1934.
- , —. Bacteria and the manufacture of tea in North East India. By P. H. Carpenter & S. F. Benton. 8vo. *Calcutta*, 1935.
- , —. Report for the years 1929, 1932, 1933. 8vo. *Calcutta*, 1930-34.
- , —. Report on a visit to Ceylon in 1935 by H. R. Cooper. 8vo. *Calcutta*, 1935.
- , —. Report of the Commission of Inquiry on the Scientific Department, 1935-36. Pp. vi+154. 8vo. *Calcutta*, 1936.
- International Tea Committee.** Memorandum relating to the tea industry and tea trade of the World. 8vo. (s.l.), 1945.
- International Tea Market Expansion Board Ltd.** Report, 1940, 1941, 1950.
- , —. Subject Report No. 4. The first year of the Tea Cars, 1940. Subject Report No. 6. Tea in factories in the United Kingdom, 1942.
- Jacobson, J. J. L. L.** Hand-book for the Cultivation and Manufacture of Tea in Java. Pp. 84. (Journ. Agric. Hort. Soc. India, vol. 13, no. 3.) 8vo. (s.l.e.a.).
- James, R.** Treatise on Tobacco, Tea, Coffee and Chocolate. Pp. 172. 8vo. *London*, 1746.
- Jameson, Wm.** Suggestions for the importation of tea makers, implements and seeds, from China, into the North Western Provinces. Pp. 6. 8vo. *Agra*, 1852.
- Johnston & Hoffmann.** The Tea industry illustrated. 8vo. *Calcutta* (s.a.).
- Judge, Charles.** Green Tea. Pp. 42. 8vo. *Calcutta*, 1920.
- Kaempfer, Engelbert.** Amoenitatum exoticarum politico-physico-mediarum Fasciculi V. 4to. *Lemgoviae*, 1712.
- , —. Five small bunches (packets) of exotic delights politico-physical-medical. With which are contained various accounts, observations and descriptions of things from Persia and further Asia; collected, with great diligence, in his wanderings through all the East. Extract p. 505. Observation 13. The story of Japanese Tea.
- , —. The history of Japan. Translated by J. G. Scheuchzer. 2 vols. fol. *London*, 1728.
- Keuchenius, A. A. M. N.** Vegetative propagation of tea. Pp. 16. 8vo. *Batavia*, 1923.
- King, George.** Remarks on the pruning of tea. (Journ. Agric. & Hort. Soc. India 3, 1871.)
- Klopstock, Fritz.** Der Tee im Britischen Weltreich. Pp. 87. 8vo. *Berlin*, 1936.
- Kydd, J. C.** The Tea Industry. Pp. 54. 8vo. *London*, 1921.
- Le Comte, Louis.** Memoirs and observations made in a late Journey through the Empire of China . . . Pp. xx+528. 8vo. *London*, 1698.

- Lees, W. Nassau.** Tea cultivation, cotton and other agricultural experiments in India. Pp. vi+395+ix. 8vo. *London*, 1863.
- A memorandum written after a tour through the Tea Districts of Eastern Bengal in 1864-65. Pp. vi+112. 8vo. *Calcutta*, 1866.
- Leesh River Debating Society.** Journal and Proceedings, 1907. Pp. 82. 8vo. *Duars*, 1907.
- Lettsom, J. C.** The natural history of the Tea-Tree. Pp. 102. 8vo. (s.l.), 1799.
- Lewis & Co.** Tea and tea blending. Ed. 2. Pp. viii+140+xxvi. 8vo. *London*, 1887.
- Linde, F.** Tea in India : a sketch, index and register of the tea industry in India. Pp. xxii+30. 4to. *Calcutta*, 1879.
- Lindgren, O.** The trials of a Planter. Pp. 206. 8vo. *Kalimpong*, 1933.
- Linnaeus, C.** Potus Theae. Pp. 16. 8vo. *Upsala*, 1765.
- Linschoten, John Huyghen van.** The voyage of John Huyghen van Linschoten to the East Indies from the old English Translation of 1598. The first book containing his description of the East in two volumes. Edited, vol. 1 by Arthur Cope Burnell ; vol. 2 by P. A. Tiele. 8vo. *London*, 1885.
- Lockter, Charles.** An account of the Trade in India. Pp. 340. 8vo. *London*, 1711.
- Louis, J. A. H.** The Gates of Thibet. Pp. 183. 8vo. *Calcutta*, 1894.
- M'Clelland, John.** Report on the physical condition of the Assam Tea Plant, with reference to Geological Structure, Soils and Climate. (Trans. Agric. Hort. Soc., India, 1837.)
- McEwan, John.** The geographical distribution of the tea plant in growth, and of its product in consumption. Pp. 19. 8vo. *Berlin*, 1899.
- Commerce in Tea. Pp. 28. 8vo. *London*, 1913.
- McGowan, A. T.** Tea planting in the Outer Himalayah. Pp. 73. 8vo. *London*, 1861.
- McK., J. W.** The manuring of tea. Pp. 20. 8vo. *Calcutta* (s.a.).
- McPherson, James.** The Neilgherry Tea Planter. Pp. vi+48. 8vo. *Madras*, 1870.
- Mallet, F. R.** On the Geology and Mineral Resources of the Darjiling District and the Western Duars. (Mem. Geol. Surv. India XI.) Pp. 96. 8vo. *Calcutta*, 1874.
- Mann, H. H.** The tea soils of Assam & Cachar. Pp. vi+138+iv+89. (Indian Tea Association.) 8vo. *Calcutta*, 1901-3.
- The ferment of the tea leaf. Parts 1-3. 8vo. *Calcutta*, 1901-4. The fermentation of Tea. Parts 1 and 2. 8vo. *Calcutta*, 1906-7.
- Red Rust. A serious blight of the tea plant. Eds. 1 and 2. (Indian Tea Association.) 8vo. *Calcutta*, 1901-4.
- The Blister-blight of tea. Pp. 12. 8vo. *Calcutta*, 1906.
- Experiments in heavy pruning in Assam. 1907.
- The tea soils of North-East India and their treatment. Pp. 284. 8vo. *Calcutta*, 1907.
- Individual and seasonal variations in *Helopeltis theivora*, Waterhouse, with description of a new species of *Helopeltis*. (Mem. Dept. Agric. India, 1, 1907.)
- The Factors which determine the quality of tea. (Indian Tea Association.) Pp. 30+30. 8vo. *Calcutta*, 1907.
- The early history of the tea industry in North-East India. Pp. 37. (Bengal Economic Journal, 1918.)
- Tea soils. Pp. 66. (Imperial Bureau of Soil Science Technical Communication No. 32.) 8vo. *Harpندن*, 1935.
- , & **Antram, C. B.** The "Mosquito-blight" of Tea. Pts. 1-6. 8vo. *Calcutta*, 1903-9.
- , —, —. The 'Red Slug' caterpillar ; a serious pest of the tea plant. Pp. 14. (Indian Tea Association.) 8vo. *Calcutta*, 1906.
- , & **Hunter, James.** Sisal-hemp culture in the Indian Tea Districts. Pp. 42. 8vo. *Calcutta*, 1904.
- Medley, A.** Tea in Assam. Pp. 46. 8vo. *Calcutta*, 1872.
- Mennell, Robert O.** Tea, an historical sketch. Pp. 64. 8vo. *London*, 1925.
- Money, Edward.** Cultivation and manufacture of tea in India. Pp. 156. (Journ. Agric. Hort. Soc. India, vol. 3, no. 2.) 8vo. *Calcutta*, 1874.
- The cultivation and manufacture of tea. Pp. xii+189. 8vo. *London*, 1878.
- Moppett, H. J.** Tea manufacture : its theory and practice in Ceylon. Pp. 98. 8vo. *Colombo*, 1922.
- Napier-Ford, G. S.** Practical notes on tea manufacture. Pp. 23. 8vo. (s.l.), 1932.
- Nieuhof, John.** Legatio Batavica ad Magnum Tartariae Chamun Lungteium, modernum Sinae Imperatorem. Pp. viii+180. 4to. *Amsterdam*, 1668.
- Okakura-Kakugo.** The book of tea. Pp. 142. 8vo. *London*, (s.a.).
- The book of tea. Pp. x+160. 8vo. *New York*, 1912.
- O'Malley, L. S. S.** Darjeeling. Pp. xiv+231. 8vo. *Calcutta*, 1907.
- Ovington, J.** An essay upon the nature and qualities of tea. Pp. 40. 8vo. *London*, 1699.
- Owen, T. C.** The Tea Planter's Manual. Pp. xxiv+162. 8vo. *Colombo*, 1886.
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- Papers relating to Tea cultivation in Assam.** Pp. 73. 8vo. *Calcutta*, 1861.
- Peal, S. E.** The Tea-Bug of Assam. Pp. 7. (Journ. Agric. & Hort. Soc. India, vol. 4 no. 1.) 8vo. (s.l.), 1873.
- Pechlin, Joannes Nicolaus.** Theophilus bibaculus sive de potu theae dialogus. Pp. 104, 8vo. *Francfurti*, 1684.
- Petch, T.** Root diseases of tea. (Journ. Roy. Bot. Gdns. Ceylon, vol. 5, no. 11, 1910.)
— The diseases of the tea bush. Pp. 220. 8vo. *London*, 1923.
- Petit, Peter.** Thia Sininsis, circa 1705. MS.
- (A) Planter.** Notes on tea in Darjeeling. Pp. ii+102. 8vo. *Darjeeling*, 1888.
- Pyke, Magnus.** Tea in modern life. 8vo. (s.l.e.a.).
- Report upon the present condition and future prospects of Tea cultivation in the North-West Provinces and in the Punjab.** Pp. iv+110. 8vo. *Calcutta*, 1857.
- Repplier, Agnes.** To think of tea! Pp. 254. 8vo. *London*, 1933.
- Riant, A.** Le Café, le Chocolat, le Thé. Pp. x+160. 12mo. *Paris*, 1880.
- Robinson, William.** Account of Assam: with a sketch of the local geography, and a concise history of the Tea-Plant of Assam: to which is added a short account of the neighbouring tribes, exhibiting their history, manners, and customs. Pp. xvi+421. 8vo. *Calcutta*, 1841.
- Royle, J. F.** Essay on the productive resources of India. Pp. x+451. 8vo. *London*, 1840.
- Royle, J. H.** Culture of tea in the Himalayas. Pp. 257-311. 8vo. (s.l.e.a.).
- Rutherford, H. K., & Hill, John.** Ceylon Tea Planters' Note-Book of useful memoranda. Eds. 3 and 4. 8vo. *Colombo*, 1892-1903.
- S., J. W.** A Tea Manual for Beginners. Pp. xii+128. 8vo. *Colombo*, 1926.
- Sabelberg, Franz.** Tee, wandlungen in der Erzeugung und Verwendung des Tees nach dem Weltkrieg. Pp. 184. 8vo. *Leipzig*, 1938.
- Scheuchzer, J. G.** See **Kaempfer, Engelbert.**
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- Shipp, H. A.** Prize essay on the cultivation and manufacture of Tea in Cachar. Pp. 36. 8vo. (s.l.), 1874.
- Short, Thomas.** A dissertation upon tea. Ed. 2. Pp. 120. 4to. *London*, 1753.
- Simond, G. G.** Tea, its effects, medicinal and moral. Pp. viii+144. 8vo. *London*, 1839.
- Smiles, Aileen.** Indian Tea. Pp. 434. (A novel.) 8vo. *London*, (s.a.).
- Stables, W. Gordon.** Tea: the drink of pleasure and of health. Pp. 112. 8vo. *London* (s.a.).
- Stalkart, J.** A short treatise on the cultivation of tea. Pp. 10. 8vo. (s.l.), 1868.
- Staunton, Sir George.** An authentic account of an Embassy from the King of Great Britain to the Emperor of China. Ed. 2. 2 Vols. 4to. *London*, 1798.
- Staveacre, F. W. F.** Tea and tea dealing. Pp. xiv+136. 8vo. *London*, 1929.
- Stoker, T. G.** Notes on the management of the tea plant. Pp. 20. 8vo. *Calcutta*, 1874.
- Stuart, C. P. Cohen.** A basis for tea selection. (Bull. Jard. Bot. Buitenzorg, Vol. 1, 1919.)
— Verslag over de selectie-werkzaamheden 1915-1920. Pp. 60. 8vo. *Batavia*, 1923.
- Sumner, John.** A popular treatise on tea: its qualities and effects. Pp. iv+44. 8vo. *Birmingham*, 1863.
- Survey and Settlement of the Western Duars in the District of Jalpaiguri, 1889-95.** Pp. 24+xiv+163+xxvi. 4to. *Calcutta*, 1895.
- Tate.** A Poem upon Thé, with a discourse on its Sov'rain virtues; and directions in the use of it for health. 8vo. *London*, 1702.
- Tea.** A Poem in three Cantos. 4to. *London*, 1743.
- Tea Cultivation in India.** Pp. 24. 8vo. *London*, 1866.
- Tea Cyclopaedia.** Collated from the last eight volumes of the Indian Tea Gazette. Pp. x+356. 8vo. *Calcutta*, 1887.
- Tea.** The romance of. Pp. 120. 8vo. *New York* [1934].
- Tea.** A new essay upon, addressed to the medical profession. Pp. 40. 8vo. *London*, 1936.
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- Torgasheff, Boris P.** China as a Tea Producer. Pp. x+252. 8vo. *Shanghai*, 1926.
- Tsiology ;** a discourse on tea. Being an account of that exotic ; botanical, chymical, commercial and medical, with notices of its adulteration, the means of detection, Tea making, with a brief history of the East India Company. Pp. vi+147. Ed. 2. 8vo. *London*, 1827.
- Tunstall, A. C.** Tea roots. Parts 1 and 2. (Indian Tea Association.) 8vo. *Calcutta*, 1916-18.
- . A stem disease of tea caused by *Nectria Cinnabarina* (Tode) Fr. Pp. 6. 8vo. *Calcutta*, 1918.
- Turner, Henry.** A treatise on tea : historical, statistical, and commercial, collated from all available sources. Pp. 42. 8vo. *London* (s.a.).
- Ukers, William H.** A trip to India, pp. 34 ; to Ceylon, pp. 38 ; to China, pp. 40 ; to Java and Sumatra, pp. 61 ; to Japan and Formosa, pp. 55. 8vo. *New York*, 1925.
- . All about Tea. 2 Vols. Pp. xiv+560 ; 568. 8vo. *New York*, 1935.
- Valentin, Michael Bernhard.** Historia Simplicium reformatata, sub Musei Museorum titulo antehac in vernacula edita, jam autem . . . a D. J. C. Beckero . . . Latio restituta, Accedit India Literata . . . Latinitate donata, longe auctior reddita, novisque figuris, illustrata a C. B. Valentini. fol. *Offenbaci ad Moenum*, 1732.
- Van der Chijs, J. A.** Geschiedenis van de Gouvernements Thee-Cultur op Java. Pp. viii+604. 8vo. *Batavia*, 1903.
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- Walsh, J. M.** Tea ; its history and mystery. Pp. 265. 8vo. *Philadelphia*, 1892.
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- Wanklyn, J. Alfred.** Tea, Coffee & Cocoa. Pp. viii+60. 8vo. *London*, 1874.
- Ward, S. R.** A glimpse of Assam. Pp. ii+220. 8vo. *Calcutta*, 1884.
- Watson, E. A.** The Tea industry in India. (Journ. Roy. Soc. Arts, 84, 1936.)
- Watson, J. F. W.** Prize Essay on the cultivation and manufacture of tea in India. 8vo. (s.l.), 1871.
- Watt, George.** The pests and blights of the tea plant. Pp. iv+467+xvii. 8vo. *Calcutta*, 1898.
- . Tea and the tea plant. Pp. 33. (Journ. Roy. Hort. Soc., 32, 1907.) 8vo. *London*, 1907.
- , & **Mann, H. H.** The principles of tea pruning. (Agric. Ledger, 1903.)
- , ———. The pests and blights of the tea plant. Ed. 2. Pp. xvi+430. 8vo. *Calcutta*, 1903.
- Whittingham, W. B.** The art of tea blending. Pp. 68. 8vo. *London* (s.a.).
- Williams, W. M.** Current discussions in Science. Pp. 92. 8vo. *New York*, 1882.
- Williams, W. M. J.** The King's Revenue ; being a handbook to the taxes and the public revenue. Pp. xvi+222. 8vo. *London*, 1908.
- Wood-Mason, J.** Report on the tea-mite and the tea-bug. Pp. 20. 8vo. *London*, 1884.
- Yule, Udny.** Notes on tea (MS.). 1937.

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